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CONTENTS

- BARTHÉLÉMY, C. Nesting Biology of *Isodontia diodon* (Kohl, 1890) (Hymenoptera: Sphecidae), a predator of cockroaches, in Hong Kong 201
- MARTÍNEZ, J. J. and A. ZALDÍVAR-RIVERÓN. A new species of *Neoheterospilus* (Hymenoptera: Braconidae: Doryctinae) from Chamela, Jalisco, Mexico 217
- RASEKH, B. and A. POLASZEK. New records of *Encarsia* (Hymenoptera: Chalcidoidea: Aphelinidae) parasitising Aleyrodidae (Hemiptera: Sternorrhyncha) in Iran, with the description of a new species. 223
- RIZZO, M. C. and M.-D. MITROIU. Revision of the European, North-African and Central Asian species of the genus *Norbanus* Walker 1843 (Hymenoptera: Pteromalidae). 228
- TURRISI, G. F. and L. VILHELMSSEN. Into the wood and back: morphological adaptations to the wood-boring parasitoid lifestyle in adult aulacid wasps (Hymenoptera: Aulacidae) 244



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Nesting Biology of *Isodontia diodon* (Kohl, 1890) (Hymenoptera: Sphecidae), a predator of cockroaches, in Hong Kong

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Abstract.—Nests of *Isodontia diodon* (Kohl, 1890) were collected in Hong Kong using trap nests. This paper reports the nest contents and brood development in 16 nests. Nesting activity was recorded *in-situ* on two traps allowing for the sequencing of prey provisioning, cell partition and nest plug construction. The following was observed: 1) this sphecid mass provisions cells with Blatellidae, mostly one species of *Balta* but also *Blatella*, a rare prey record for the genus, 2) the cell partition and nest plug material were formed from fine plant pubescence rather than the grass and debris assemblage generally used in the genus, and 3) approximately 18% of all cells were parasitized by Diptera, and total brood mortality was approximately 34%.

Key words.—Blattelidae, prey, construction material, larval development, mortality, nesting behaviours, trap nest, Sarcophagidae, Phoridae

Isodontia diodon (Kohl, 1890) is a widely distributed species, ranging from Nepal to China and peninsular Malaysia and is common throughout Hong Kong. The taxonomic status of this species was reviewed by Hensen (1991), but nothing was known about its nesting habits. This paper reports the observations on trap nests of this species in Hong Kong between 2006 and 2009. Voucher specimens have been deposited at the Department of Entomology, California Academy of Science, San Francisco, USA.

MATERIALS AND METHODS

The traps consisted of hollow bamboo canes that were cut so that one end was closed by a nodal septum, they were of various length and diameter. Four to seven segments were bundled together and hung from low branches on bushes and trees, the bundle orientation was random but all were in shaded or semi-shaded conditions. They were inspected daily when wasps were active, less so when no activity was observed. Active traps were collected after completion of the nest and for rearing -

sealed in plastic "Ziploc" bags. Traps were placed in and collected from two localities: 1) the author's garden: Hong Kong; Pak Sha O; UTM: 50Q KK 237 850, alt. 70 m above sea level (marked as PSO). The garden is a reclaimed land on an abandoned *Citrus* orchard, adjacent to a healthy 50+ years old secondary forest, at the bottom of the Northern slopes of a small hill and 2) a semi-active orchard of an old village: Ha Tin Liu Ha; UTM: 50Q KK 058 849, alt. 60 m above sea level (marked as HTLH) The orchard is located on the northern foothills of Tai Mo Shan and is adjacent to a healthy 60+ years old forest.

Quantitative data pertaining to brood, parasites, prey, cells dimensions, etc. of 16 traps totaling 50 cells were obtained at tube opening followed by daily inspection of larval development and prey consumption of 13 active larvae in five traps.

Details of wasp activities were also recorded *in-situ* on two traps (later collected) in early June 2009. These observations were carried out at the beginning of the wet monsoon period in Hong Kong (June), characterized by violent rain downpours,

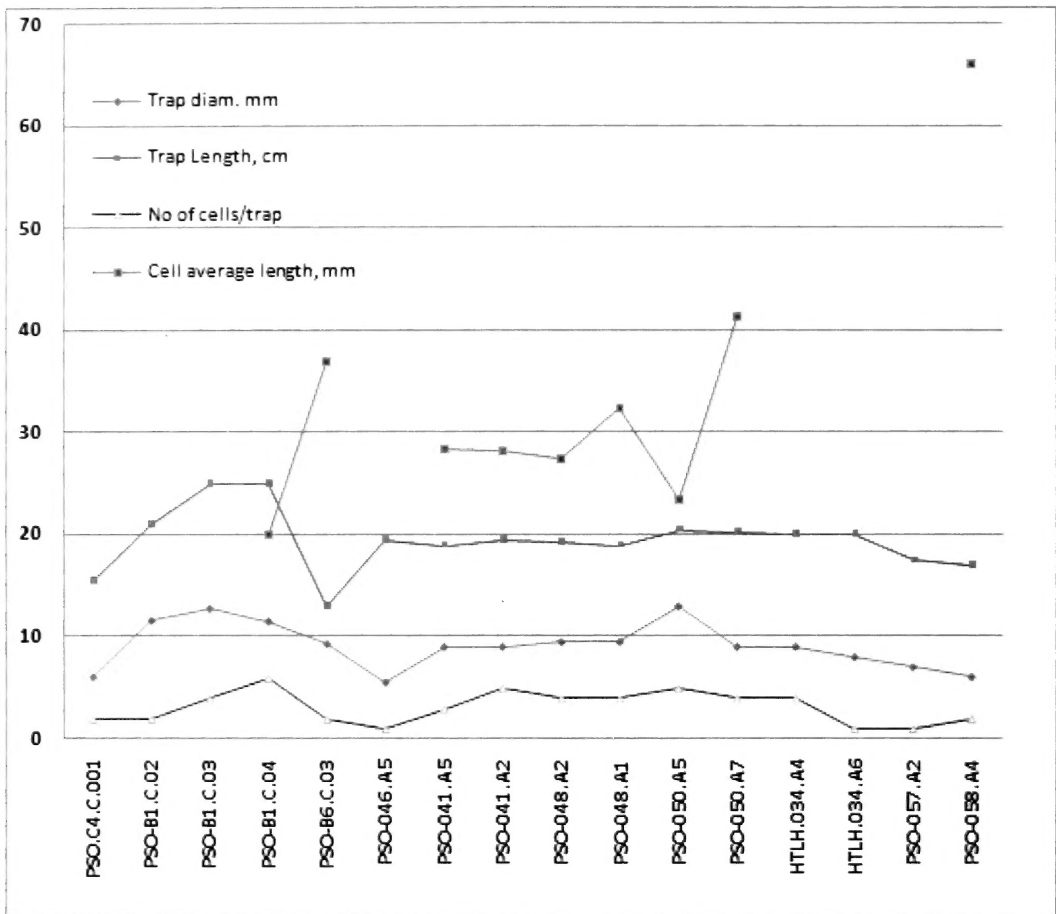


Fig. 1. Comparison between various trap parameters.

alternating with periods of heat, and sunshine or overcast.

RESULTS AND DISCUSSION

Description of nests of *Isodontia diodon*

Nest architecture.—Each nest contained from one to six cells (average=3.13, $n=16$). The cells were 20–50 mm long (not counting the last cell) (average=29.85 mm, $n=26$), except the last cell was generally much longer (average=68.33 mm, $n=9$). It was noted that cell 1 was longer than cell 2, which in turn was longer than cell 3, and so on. The cell length was not correlated with the trap diameter or length; however there was an apparent correlation between trap diameter and the number of cells in each

trap and a weak correlation between trap length and cell number; the cell number increasing or decreasing accordingly (Table 1, Fig. 1). The recorded trap diameters varied from 5.5 to 12.8 mm (average=9.11 mm; $n=16$) (Tables 1, 2). The nests can be characterized by the following: 1) no vestibular or intercalary cells, 2) the outer end of the most external cell is always defined by the nest plug, 3) the innermost cells did not necessarily start from the bottom of the tube, but could be initiated anywhere along its length, and 4) the inner end of the first cell was always padded with cell partition material (Fig. 5).

The nest plug and cell partitions were constructed out of the same material, very

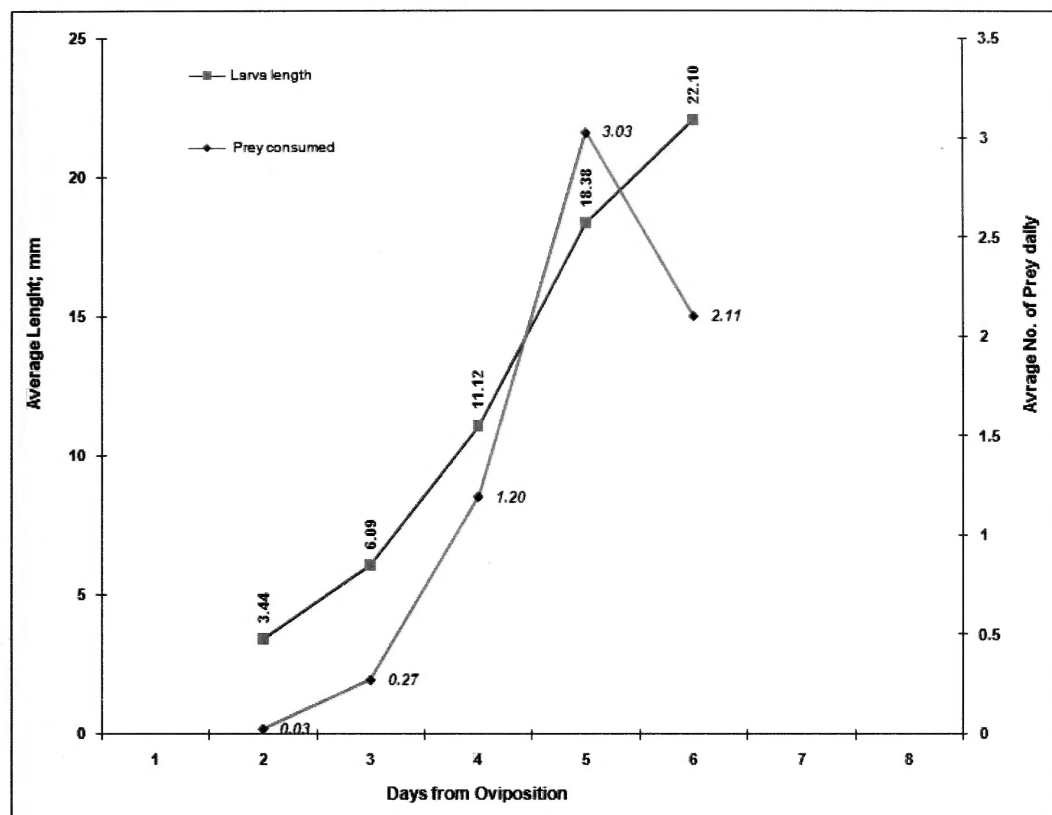


Fig. 2. Growth and prey consumption.

fine plant pubescence from three sources (Figs 12, 13): 1) the young shoots of *Mallotus paniculatus* Muell. Arg. (Euphorbiaceae), a common fast growing tree in Hong Kong's old village grounds, 2) the underside of leaves of *Vitis balanseana* Planch, 1887 (Vitaceae), a vine, and 3) an un-identified plant (found only in the HTLH traps).

The material is compacted and shaped into an irregular and loose cell partition, 2–5 mm thick, and a cylindrical closely compacted plug, 15–25 mm long, always finished flush with the tube entrance with a slight concavity of the outer face.

Isodontia diodon constructs and provisions multi-cellular nests typical of the genus (Bohart and Menke 1976). The wasp uses exclusively plant pubescence for construction of nest plugs and cell partitions, a unique record for the genus, other

species preferring grass blades and occasionally leaves, rotten wood fibers, debris and/or a mixture of these materials (Krombein 1967). The shape of the mandibles of this wasp, short, straight and bidentate apically, is unique in the genus and is most likely an adaptation for this material.

Prey and oviposition.—Each cell was mass-provisioned with four to nine specimens (average=5; n=50) of Blatellidae, with matures much more common than nymphs (Table 2). The majority of the prey (60%) were *Balta* sp. 1 (Dictyoptera: Blatellidae), a small local woodland and grassland cockroach (a sampling of nine prey from two cells found all females), 32% were adults (males and females) of *Blatella bisignata* (Brunner von Wattenwyl, 1893) with occasional immature; a very common grassland roach locally. Finally, a little over 7% were small unidentified Blatellidae of

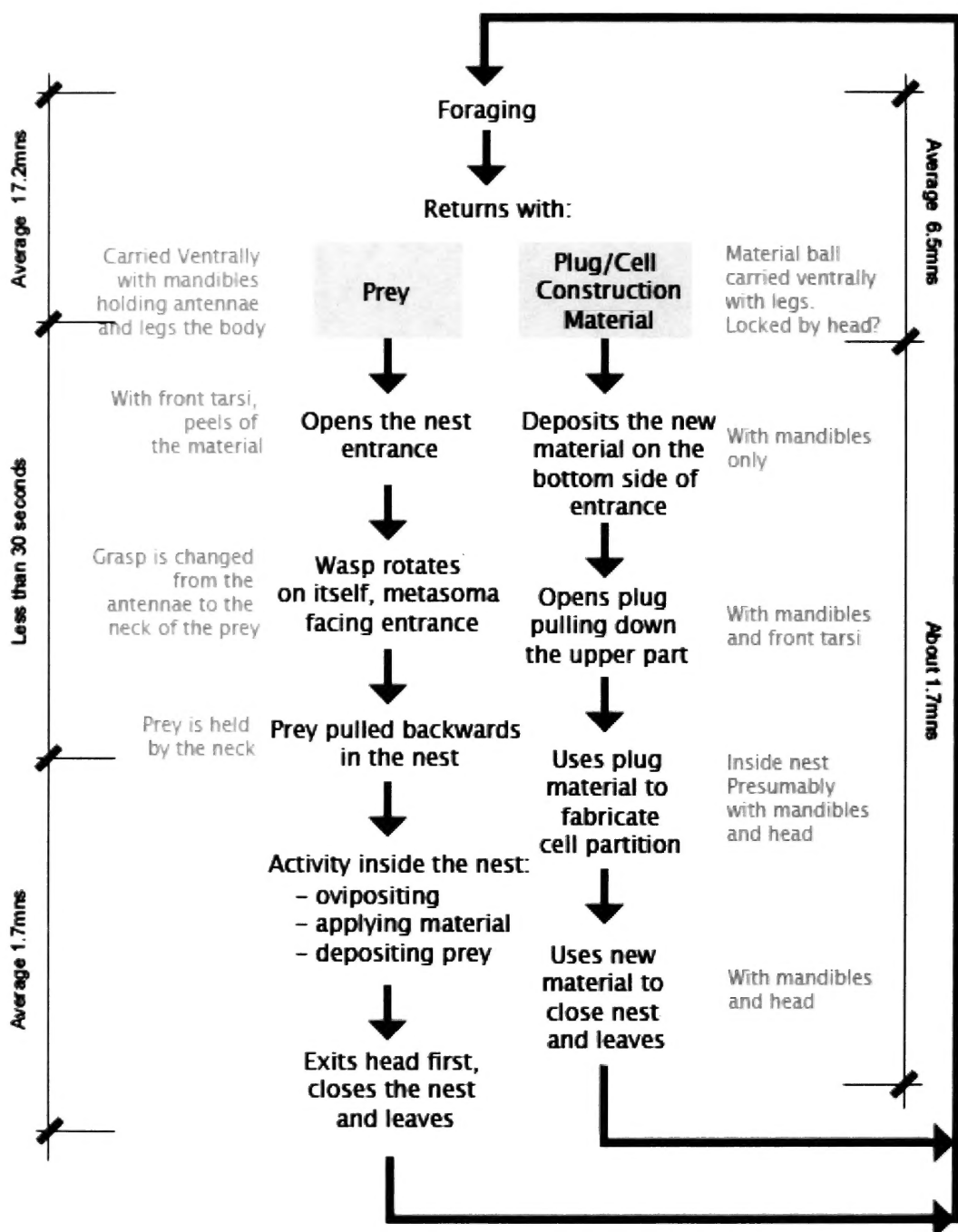


Fig. 3. *Isodontia diodon*; on-nest behavioral sequences.

at least three different species in two genera. All the prey were lightly paralyzed (able to move their appendages and defecate). They were closely packed headfirst

and lengthwise in each cell. See Fig. 6 for a typical contents of trap nest at collection.

Eggs were laid latero-ventrally on the prey, the anal end attached close to the fore

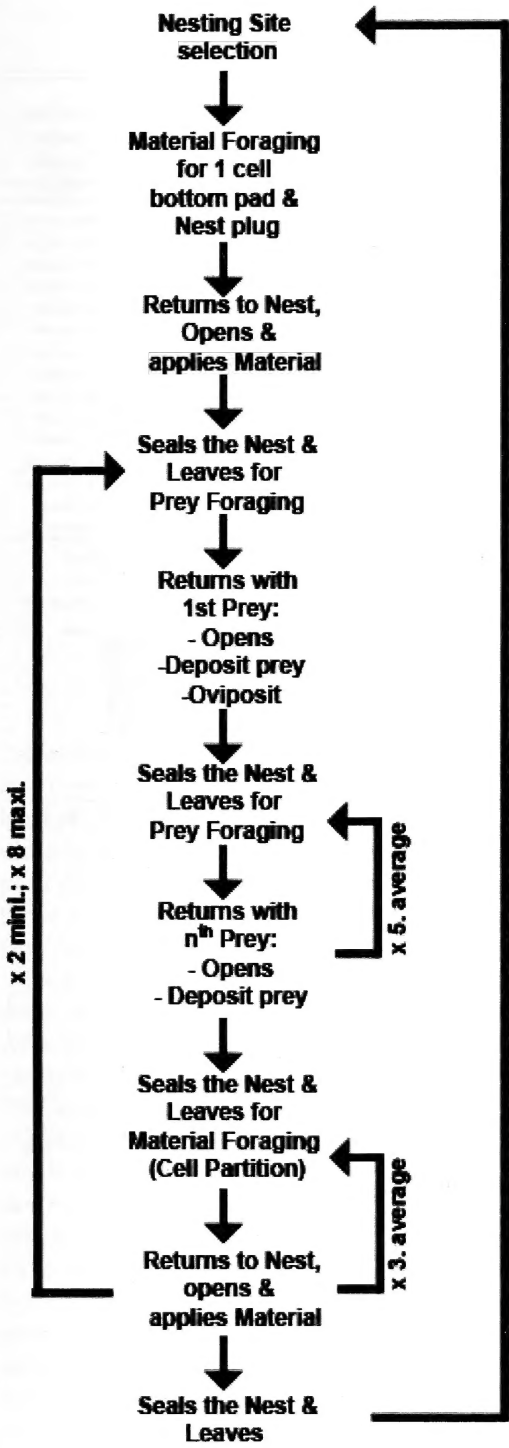


Fig. 4. *Isodontia diodon*; daily activity sequences.

or mid coxae joints (Fig. 6). This differs from other *Isodontia* spp., which generally prefer the ventral cephalothoracic suture as described by Krombein (1967). All the eggs (and early first instar larvae) were found to be located at the bottom of the cell and were most likely laid on the first prey placed in the cell as has been previously noted for other *Isodontia* spp. (Krombein 1967; O'Neill 2001).

The larvae of *I. diodon* have a rather specialized diet (only Blattidae) with about 92% of the prey represented by just two species, *Balta* sp.1 and *Blatella bisignata*, mostly adult females. Cockroaches are only known to be used by one other species of *Isodontia*; Iwata (1939) mentions *I. formosicola* (Strand 1913) provisioning with Blattidae (Bohart and Menke 1976, translated from Japanese).

Brood.—Each cell contained a single egg, larva, or pupa. Upon hatching the first instar larva immediately started feeding externally off the soft tissues at the fore coxa/thoracic articulation of the prey. Later the larva partially penetrated the body cavity at the same spot to feed (Fig. 6). Having consumed the first prey, the larva then fed on the other prey at various points on their bodies, as it was now large enough to handle harder tissues. The penetration of the larvae in the body cavity for feeding was also noted by Krombein (1967) for *I. auripes*, albeit on a different prey.

Hatching time from oviposition was 2–3 days (average=2.06, n=18), while the development time from oviposition to prepupal larva was 5–7 days (average=6.21, n=14) (Table 4), the grub nearly doubling in length daily for the first four days after hatching (Figs 2, 8, Table 4) in agreement with observations by Krombein (1967) for other *Isodontia* spp. This short development time may explain why the prey were lightly paralyzed, as there is no need of a deeper/longer immobility in relation to the feeding time. The quantity of prey item consumed followed the rapid growth rate

Table 1. Trap and cells dimensional data.

	Trap data			Cell data							
Trap ref.	Trap diam. (mm)	Trap length (cm)	No of cells/trap	Cells mean length (mm)	Cell 1 (mm)	Cell 2 (mm)	Cell3 (mm)	Cell 4 (mm)	Cell 5 (mm)	Cell 6 (mm)	Last cell mean length (mm)
PSO.C4.C.001	6	15.5	2								
PSO-B1.C.02	11.6	21.05	2								
PSO-B1.C.03	12.8	25	4								
PSO-B1.C.04	11.5	25	6	20	20	20	20	20	20	125	
PSO-B6.C.03	9.3	13	2	37	37	90					
PSO-046.A5	5.5	19.5	1								
PSO-041.A5	9	19	3	28.33	35	28	22				
PSO-041.A2	9	19.5	5	28.25	33	35	25	20	56		
PSO-048.A2	9.5	19.3	4	27.33	30	25	27	18			
PSO-048.A1	9.5	19	4	32.33	40	30	27	80			
PSO-050.A5	13	20.5	5	23.5	22	20	20	32	98		
PSO-050.A7	9	20.2	4	41.33	50	40	34	55			
HTLH.034.A4	9	20	4								
HTLH.034.A6	8	20	1								
PSO-057.A2	7	17.5	1								
PSO-058.A4	6	17	2	66	66	71					
Mean	9.11	19.44	3.13	29.85	37	28.29	25.5	24	20	125	68.33

Denotes no data

Denotes last cell; data not counted when averaging values of the other cells

of the larva (Fig. 2), although it decreased from three prey per day on the third day after hatching to two prey per day on the fourth, the larva still growing between the third and fourth day. At which point it stopped feeding even though prey could be left partially consumed.

The pre-pupating larva spun a complete double-layered cocoon, slightly adherent to the cell walls, only attached by a few strands of silk (Figs 7, 9) in approximately one day; in the process, the cell partition material as well as prey remnants were used to cover the outer layer, making it difficult at times to distinguish the limits of the original cell. The whitish outer layer was coarsely woven and flexible, but resistant to shear. The inner layer was

finely woven, more rigid, brittle and brownish. The pupation period lasted approximately 24–29 days from oviposition (average=25.92, n=13) (Table 4). Over wintering was observed on one trap (PSO-051.A1) which contained one cell with a cocoon. The trap was collected on 2 December 2009 and at time of drafting (25 March 2010) the specimen was still in pre-pupal/pupal stage.

During the larval growth, accumulation of both uric acid and feces was visible through the integument, white spots marking the former, and the latter as a growing sac of liquid at the anal end (Fig. 7). The meconium is later discharged into the posterior end of the cocoon, possibly a little after the inner layer has been spun.

Table 2. Traps details & content, larval death and sex ratio.

	Trap details					Brood at trap opening				Prey details					Parasitism	Larval death		Sex ratio				
Trap reference	Trap set	Trap Collected	Diameter (mm)	Length (mm)	No. of cells	Eggs	Larvae	Pupae	Cells with no eggs	No. of prey	Baita sp.	<i>B. blagnata</i>	small Blattellidae sp1	small Blattellidae sp2 *	Total Prey No.	No. of cells	No. of cell parasitized	Active spec at opening	Dead specimens	No. of cells	Female	Male
PSO-C4C.001	15/vi/06	10/vii/06	6	155	2	0	1	1	0													
PSO-B1.C.02	15/vi/08	02/viii/08	11.6	210.5	2	0	0	1														
PSO-B1.C.03	15/vi/08	30/viii/08	12.8	250	4	0	1	3	0													
PSO-B1.C.04	15/vi/08	05/vii/08	11.5	250	6	0	6	0	0	34								6	2	4	2	2
PSO-B6.C.03	15/vi/08	05/vii/08	9.3	130	2	0	2	0	0	12						2	0	2	0	2	1	1
PSO-046.A5	06/vi/09	21/vi/09	5.5	195	1	1	0	0	0	5	4	0	1	0	5	1	0	1	0	1	1	0
PSO-041.A5	06.v.09	14.vi.09	9	190	3	3	0	0	0	13	13	0	0	0	13	3	0	3	1			
PSO-041.A2	06.v.09	17.vi.09	9	195	5	2	2	0	1	28	25	1	2	0	28	4	1	4	0	4	1	3
PSO-048.A2	22.v.09	23.vi.09	9.5	193	4	0	1	0	3	27	16	10	0	1	27	4	2	1	0			
PSO-048.A1	22.v.09	25.vi.09	9.5	190	4	1	0	0	3	22	8	12	0	2	22	4	2	1	0			
PSO-050.A5	22.v.09	28.vi.09	13	205	5	0	5	0	0	34	16	17	1	0	34	5	0	5	1	4	4	0
PSO-050.A7	22.v.09	02.vii.09	9	202	4	2	1	0	1	29	19	8	0	2	29	3	0	3	0	3	3	0
HTLH.034.A4	01.v.09	10.vii.09	9	200	4	0	1	3	0	29						4	0	4	1	3	2	1
HTLH.034.A6	01.v.09	10.vii.09	8	200	1											1	1					
PSO-057.A2	15.vii.09	26.vii.09	7	175	1	0	1	0	0	3	2	1	0	0	3	1	0					
PSO-058.A4	15.vii.09	03.viii.09	6	170	2	1	1	0	0	14	3	7	2	2	14	2	0	2	0	2	1	1
Totals					50	10	22	8	8	250	106	56	6	7	175	34	6	32	5	23	15	8
Mean			9.11		3.13					20.83												
Percentages									17.02		60.57	32.00	3.43	4.00		17.65		15.63		65	35	

Notes:

Denotes lack of data for that particular instance

* Data represents at least two un-identified species and nymphs.

Voltinism.—*Isodontia diodon* is active from end of May until end of August at least. Field observations have shown individuals nesting during three distinct time periods, separated by periods of at least three weeks were no activity in the field was recorded.

Quantitative data relating to oviposition and emergence of adults were obtained with nine traps collected in the author's garden, a relatively small study area (Table 5). The table visualizes, three active clusters: third week of May, mid-June/July and end July/early August, separated by two periods where no oviposition was recorded (third week of May until 14 June; 2 July until 24 July), in correlation with the field observations. Casual records of this species tend to show that it normally emerges from over-wintering in early to mid June rather than mid May. From the combined field and rearing observations, it can be inferred that *I. diodon* may have three generations a year in Hong Kong. In deed the single oviposition recorded in May 2009 might be exceptional, but the last

two ovipositions on Table 5 led to an emergence around the 28 August, suggesting an additional third generation that over-winters as a pre pupae and emerging in May–June the following year.

Theoretically, the brood development time of 26 days would allow for three to four generations within the activity period (June to August) of the wasp.

Sex ratio.—The sex ratio was obtained from seven traps containing 23 cells in total. While in individual nests the sex ratio can be overwhelmingly biased, with either a majority of females or males, the overall sex ratio was 65% females and 35% males (Table. 2).

Natural enemies, nests associates, and larval mortality.—Six out of 34 cells analyzed (18%) contained parasites (Table 2). The content of the infested cells was emptied and reared separately for observation. Two traps (PSO-041.A2 and HTLH-037.A6) were infested by maggots of *Amobia quatei* Kurahashi (Diptera, Sarcophagidae, Miltogramminae; L.E.N. Sijstermans, det.), a sub-family commonly asso-

Table 3. Activity counter.

Activity	Total duration (min)	%	Mean duration (min)	Incidence (n)
Material Foraging	56	21.54	6.22	9
Prey Foraging	86	33.08	17.2	5
Open/ Activity in tube/Seal	21	8.08	1.75	12
Unknown	97	37.31	13.86	7
Total	260	100		

ciated with cleptoparasitism in many solitary aculeate wasps (Krombein 1967, 1991; Evans and Eberhardt 1970; O'Neill 2001). The remaining two traps (PSO-048.A1 and A2), which were part of the same bundle, had been attacked by a very small *Megaselia* sp. (Diptera, Phoridae; Paul Beuk det.), which are also known parasitoids of aculeates (Genaro 1996; O'Neill et al., 2007).

At collection (17 June 2009), nest PSO-041.A2 contained five cells. Cell 1 and 2 had two active wasp larvae, cell 3 and 4 had one wasp egg each and cell 5 only contained maggots feeding on provisioned prey (Fig. 10). On 4 July 2009 about ten adults of *Amobia quatei* emerged from the nest. The pupation of the fly larvae occurred outside the nest in the Ziploc bag.

The only cell of nest HTLH-037.A6 contained no wasp brood, but several Diptera pupae and prey remnants towards the tube entrance. Adults of *Amobia quatei* emerged from these pupae on 15 July 2009.

At collection (25 June 2009), nest PSO-048.A1 contained four cells, of which only cell 2 had a wasp egg, while cells 1, 3 and 4 contained prey but no wasp eggs. From a superficial inspection, cell 1 contained numerous small dipteran eggs (<0.5 mm long) laid on the prey, the tube surfaces, and the partition material (Fig. 10); small adult flies were also seen running on the trap surface. After about 24 hours, numerous very small (1 mm long) maggots hatched and started feeding on the stored prey. The fly larvae were removed from the trap and reared separately, pupating in

about 72 hours without having finished the provisions that I had provided. Adult *Megaselia* sp. started emerging on 8 July 2009. The wasp egg hatched, the larva started to develop and later died in early development stages for no apparent reasons.

At collection (23 June 2009), nest PSO-048-A2 contained four cells; cell 2 had a wasp egg, cells 1, 3 and 4 were provided with prey but no wasp eggs. Similarly, Diptera eggs were seen on prey of cell 1 along with adult individuals. The infested content was reared separately and adult *Megaselia* sp. emerged on 14 July 2009. The wasp egg hatched, the larva survived, pupated and emerged on 18 July. In all cases of suspected cleptoparasitism, the wasp egg was absent from the infested cell, suggesting that the fly had consumed the eggs.

The status of *Amobia quatei* Kurahashi as a cleptoparasite of *I. diodon* has been established in the literature and confirmed in this study. On the other hand, the biology of *Megaselia* sp. is more difficult to establish. The genus has been recorded by Genaro (1996) "emerging as scavengers" from nests of *Sceliphron jamaicense* (Fabr.) in Cuba, but not evidently as cleptoparasites.

More studies are required to ascertain the biology of this fly, but the presence of adult *Megaselia* in the cells when opening the traps indicates that the flies were able to penetrate the nest while the wasp was building it. It is unclear whether the adult fly is responsible for the wasp egg disappearance in the infested cells, although it cannot be the larva as only Diptera eggs and adults were found at trap opening (nest completion).

For *Amobia quatei*, I make the following assumptions based on circumstantial deductions and known biology of Miltogramminae (Krombein 1967; Evans and Eberhardt 1970; O'Neill 2001): The fly does not penetrate the tube (always closed at the wasp's departure) through the plug, as no

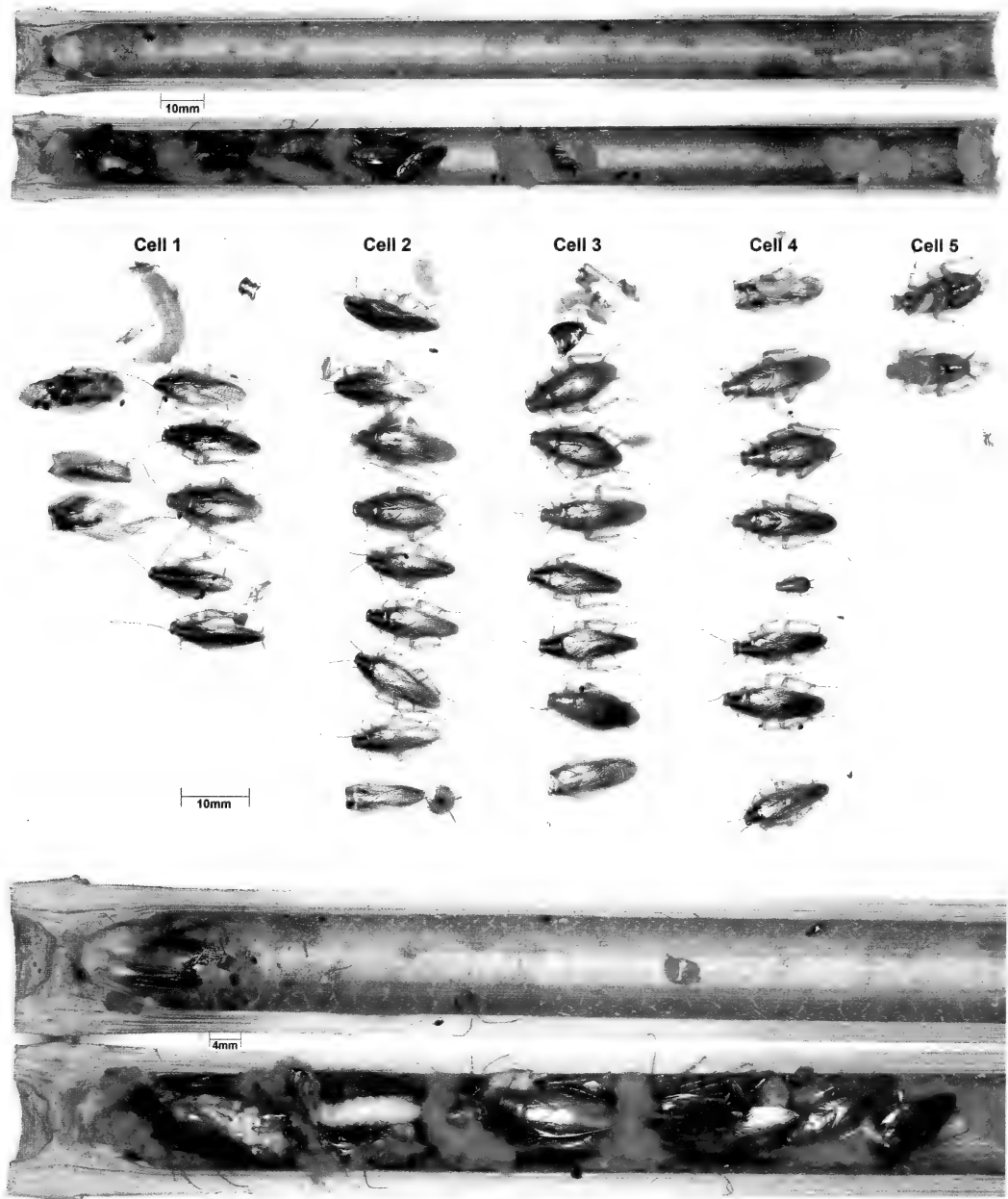


Fig. 5. Nest Trap PSO-050.A5; Top two plates: content at opening. Bottom picture: the same tube two days later. Photo Author.

trace of such action was observed when the tubes were opened. The only time when the nest is open is when the wasp is inside and an intruder of that size would be promptly chased away. This leaves two

possibilities: At capture of prey, the fly oviposits on the prey and/or, the fly enters the nest when the wasp is busy opening the nest or rotating or pulling the prey in.

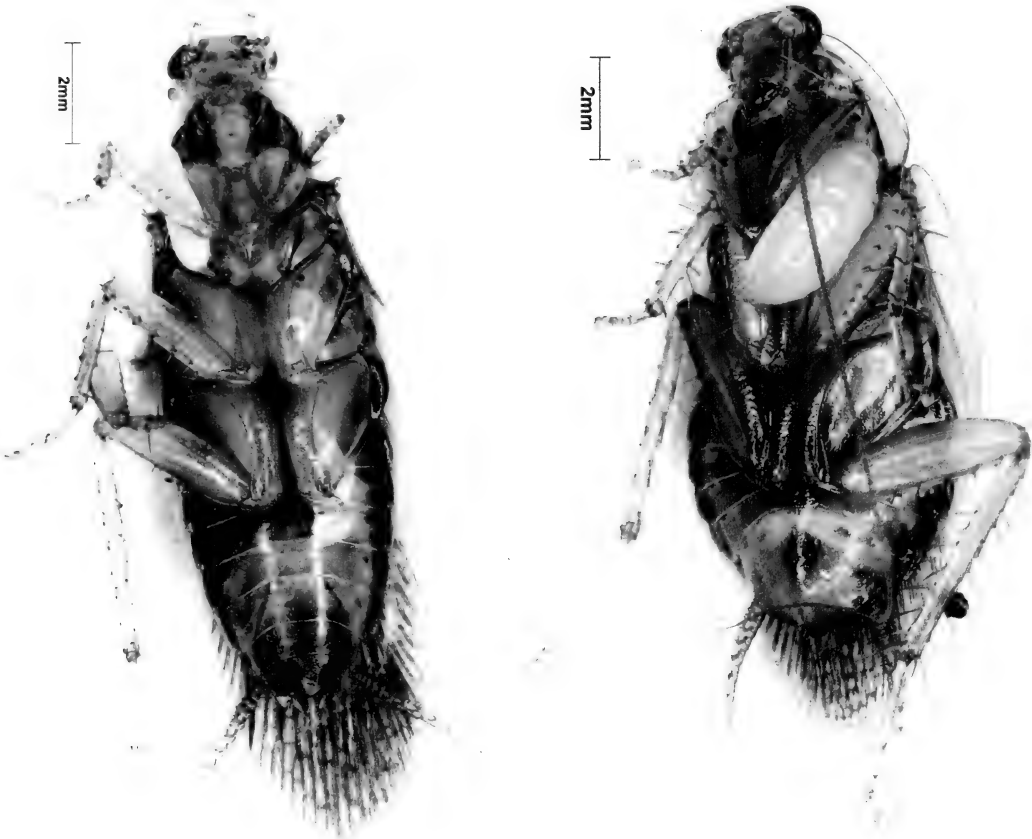


Fig. 6. Oviposition site and early instar larvae feeding through the coxa/thoracic suture. Photo author.



Fig. 7. Nest Trap PSO-C.B1.03: Cocoon and mature larva. Photo author.

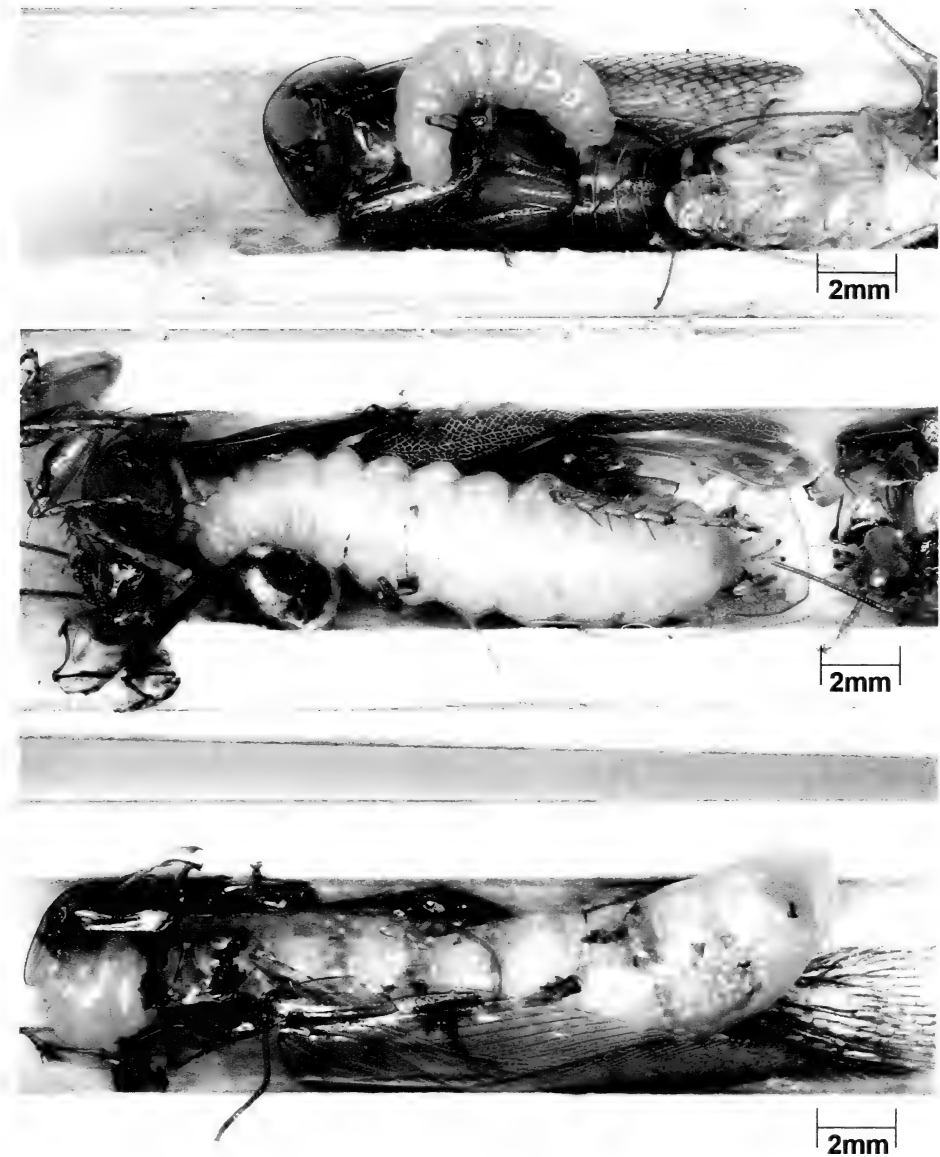


Fig. 8. Larva development over three days. From top to bottom: three four, and five days after oviposition. Pictures at the same scale. Photo author.

In addition to Diptera, small white-bodied Acari were recorded regularly, either on the prey or the wasp larvae (PSO-048.A2). It was not clear whether these Acari originated from the prey, then migrated to the larvae or were introduced by the mother sphecids. The mites did not kill the host; it is unknown whether they

feed on the sphecids or on other material in the nest.

Larvae and pupae sometimes died during the developmental stages, with no apparent connection to parasites or nest associates in fact the cause of mortality remains unknown. Out of 32 egg/larvae or pupae alive at tube opening, five died

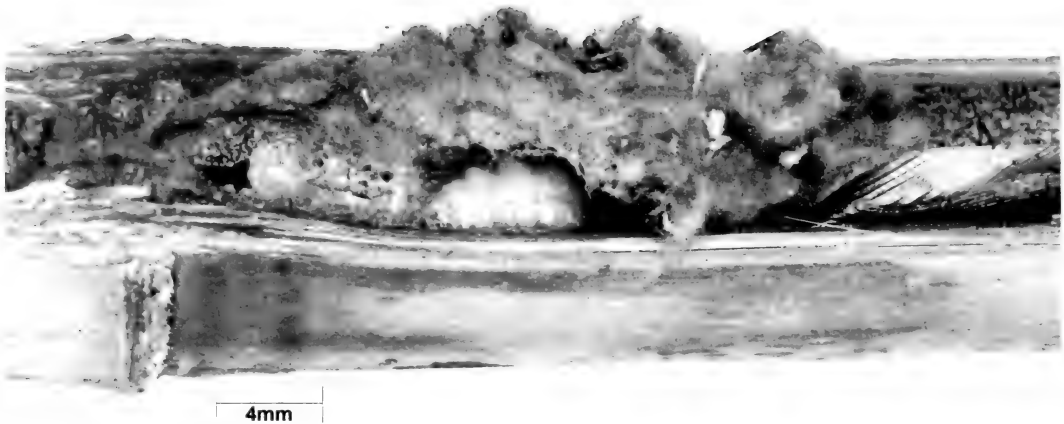


Fig. 9. Larva spinning the first layer of the cocoon. Photo Author.

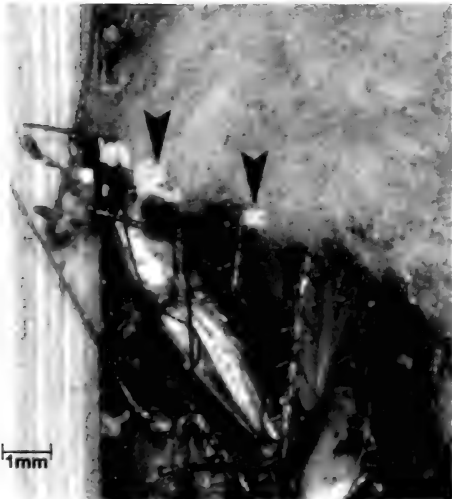
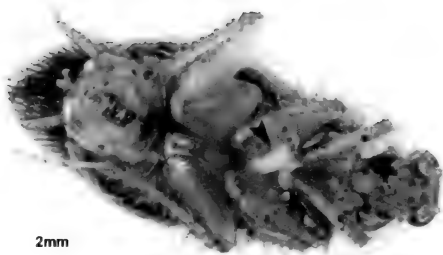


Fig. 10. Instances of infestation. Top plate, PSO-041.A2 Cell 5, maggots of *Amobia quatei*, feeding on the wasp provisions. Bottom plate, PSO-048.A2 Cell 1, eggs of *Megaselia sp.* on cell partition. Photos author.

before maturity, a mortality of nearly 16% (Table 2).

When larval death is combined with the mortality due to parasitism, one third (33.27%) of all larvae/pupae died in the nest.

Field Observations

Transportation of both prey and nest construction material were observed over two days at nests PSO-041.A5 and A2. Four major behaviors were observed at the vicinity of the nest: 1) return from prey foraging trip, 2) return from construction material foraging trip, 3) opening nest/activity inside nest/sealing nest, and 4) other activities referred to here as "unknown".

Table 3 summarizes the time spent by the wasp for each group on trap PSO-041.A5 over a period of 4 h 20 mns of *in-situ* observation.

Within the four major behavioral activities listed above, I was able to identify and provide a sequencing of sub-behaviors pertaining to landing, prey/material carriage/provisioning, entrance opening/closing and plug/cell partition building (Fig. 3) and fit them within a proposed sequence of daily activities (Fig. 4). Prey

Table 4. Mean larval growth, prey consumption and development time.

Days after oviposition	Mean larvae length (mm)	Mean cumulative prey consumed	Mean hatching time (days)	Mean larval time (days)	Mean pupation time (days)
			2.06	6.21	25.92
2	3.44	0.03			
3	6.09	0.27			
4	11.12	1.2			
5	18.38	3.03			
6	22.1	2.11			

provisioning is illustrated as a photographic sequence (Fig. 11). Activity ceased at early night fall and the wasp did not take refuge in the nest.

Prey and material transportation.—The length of prey-foraging trips were variable from 7 to 27 minutes (average=17.2 minutes, n=5, often exceeding 20 minutes) (Table 3). During approximately four hours of observation, one wasp brought back five prey (enough for one cell). Foraging for cell

partition material was completed in about six minutes per trip (average=6.22 minutes, n=9). The wasp repeatedly came back from foraging trip without a catch or nest material, in which case she shortly examined the nest and left. Approximately 37% of the time was spent on such trips (“unknown” category), while the wasp spent over 90% of the time away from the nest.

Prey and material transportation require some discussion. First, when landing the wasp always faces the entrance; the prey is locked ventrally. However, as she pulls the prey backward, entering the tube metasoma first, she needs to rotate her body to grasp the item by the neck. To do so the female opens her mandibles and let go of the prey while holding it in place with the tarsi (and possibly the antennae). The wasp then rotates so that she is head down over the prey and allows the roach to slide down until she can seize the cephalothoracic constriction by the mandibles. This

Table 5. Oviposition & emergence time sequence of nineteen cells in nine traps at Pak Sha O.

	May	June					July					August						
	21/05/2009		14/06/2009	19/06/2009	22/06/2009	24/06/2009	25/06/2009	01/07/2009	02/07/2009	10/07/2009	11/07/2009	18/07/2009	20/07/2009	24/07/2009	26/07/2009	27/07/2009	28/07/2009	25/08/2009
HTLH-033.A4								•	-----									
								•	-----									
								•	-----									
								•	-----									
								•†	-----									
PSO-041.A2			•	-----														
			•	-----														
			•	-----														
			•	-----														
			•†	-----														
PSO-041.A5			•†															
PSO-046.A5	•	-----																
PSO-048.A1								•†										
PSO-048.A2					•	-----												
PSO-050.A5								•	-----									
								•	-----									
								•	-----									
								•	-----									
								•†	-----									
PSO-050.A7									•	-----								
									•	-----								
									•	-----								
PSO-057.A2														•†				
PSO-58.A4																•	-----	
																•	-----	

- Notes:
- Denotes oviposition
 - Denotes emergence of adult
 - † Denotes brood death during development

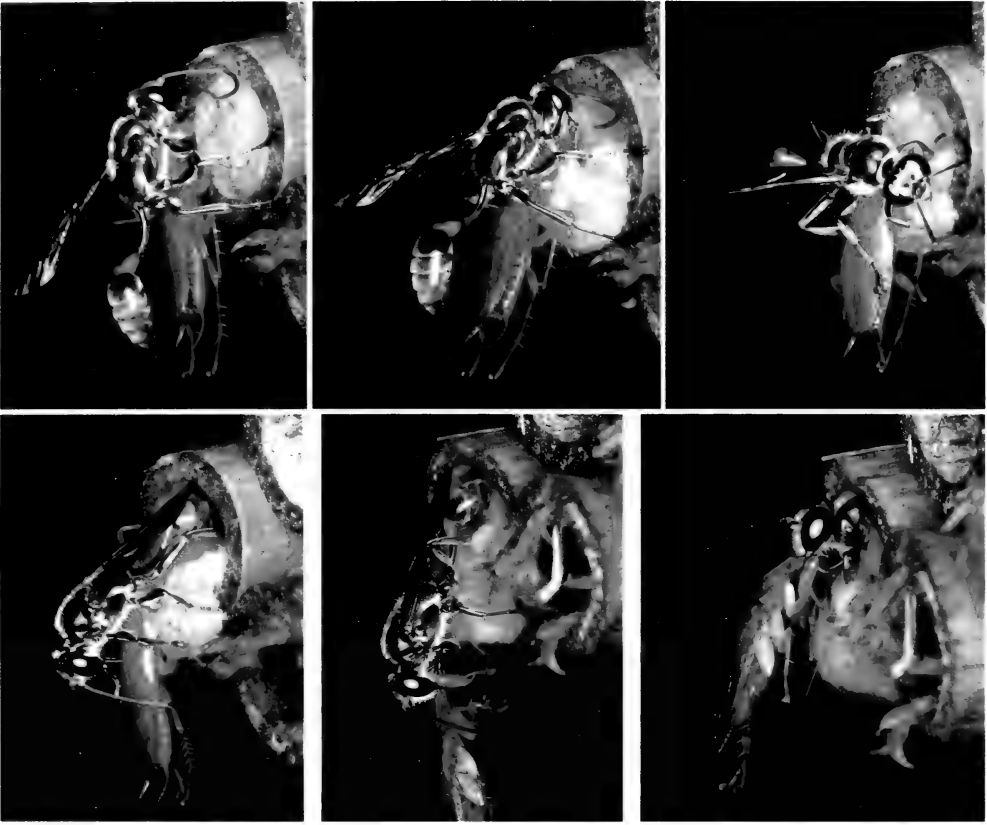


Fig. 11. Photographic sequence of prey provisioning. Photos author.

behavior risks losing prey, which nearly happened on one of the foraging return trips (Fig. 11). Second, before leaving the nest for foraging (material or prey) the

wasp closes the nest entrance with a thin temporary plug a few millimeters thick, more of an operculum than a plug. To open the entrance the wasp does not release the

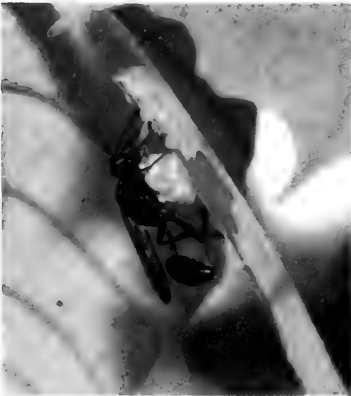


Fig. 12. *Isodontia diodon* collecting material on *Mallotus paniculatus*. Photo John X.Q. Lee.



Fig. 13. *Isodontia diodon* collecting material on *Vitis balanseana*. Photo author.

prey that she holds with the mandibles. Instead, she uses the front tarsi to peel off and fold down the top part (flap) of the operculum, creating a sufficiently large entrance. This enables an easy closure before departing by just lifting the bend flap, which is compacted with the mandibles and head at the tube entrance.

Nest plug and cell partition construction.—Foraging for nest materials was observed for a single female working on the setae found on the underside of leaves of *Vitis balanseana* (Fig. 13). The material was scrapped and kneaded with the mandibles to the texture of cotton, formed into a near spherical ball and transported to the nesting site held ventrally with the forelegs.

When the wasp constructed a nest plug, the material was transferred to the mandibles upon landing and simply applied to the working area, with much compaction of the head and mandibles. The cell partition construction sequences were more complex. On landing, the wasp deposited the new material outside of the nest entrance; she then opened the plug and used the old plug material to construct a new partition inside. A new plug was then constructed with the new material. Compaction was achieved by rapid movements of the head. Two to four foraging trips were necessary to complete a single cell partition, nest plug construction was not observed but from the thickness of this element it can be inferred that at least four times as many trips were necessary for its construction.

From the combined data of prey and material transportation and application it can be inferred that a complete nest (5 cells) would take approximately two days (working 10–12 h per day), including the time for construction of partitions and plugs. Actual observations of other traps found that some nests were completed in two to three days. Adverse weather conditions (heavy rainstorms, mainly overcast) certainly can influence this time period.

CONCLUSIONS

The nesting biology of *I. diodon* is rare for the genus by both the nature of the prey provisioned for the larvae and the materials used for nest construction. This inevitably raises the question of how and why the traits of provisioning Orthoptera and using grass for nest construction in other *Isodontia* spp., diverged. The unusual prey selection of *I. diodon* is not explained by the scarcity of Orthoptera nor the abundance of Dictyoptera. Locally, other species of *Isodontia*, such as *I. nigella*, successfully prey on Orthoptera, while *Balta* sp. is not particularly common, as evidenced by the paucity of my collecting records and inferred by *I. diodon*'s long foraging trips. The nesting material used is neither very abundant nor easy to extract compared to grass material, however the shape of the mandibles (abnormally slender and apically bifid rather than broad and tridentate in the other species) may offer an explanation to the specialized nature of the nest material.

Future observations on East Asian *Isodontia* are necessary to establish whether the observed habits of *I. diodon* are rare or commonly shared with some other congeners.

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I am extremely grateful to the various people without whom much of this paper would have been impossible or far more incomplete, particularly Wojciech J. Pulawski, Curator, California Academy of Science, San Francisco, USA, who identified the wasp species and gave valuable advice on the manuscript; Robert L. Zuparko, also California Academy of Sciences, for his very meticulous linguistic review of the manuscript; two anonymous reviewers who greatly contributed to the form and rigor of the final document; Darren Mann, Assistant Curator, Hope Entomological Collection, Oxford University, Oxford, United Kingdom, for the identification of prey species; Liekele Sijstermans, University of Amsterdam, Amsterdam, Netherlands, who identified the Diptera cleptoparasites and finally Paul Beuk, Natural History Museum of Maastricht, Maastricht, Netherlands, for the difficult task of identifying the micro-Diptera. Additionally, I would like to thank John X. Q. Lee, Hong Kong, China, for the photograph illustrating the foraging of this species.

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A new species of *Neoheterospilus* (Hymenoptera: Braconidae: Doryctinae) from Chamela, Jalisco, Mexico

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Abstract.—A new species of *Neoheterospilus*, *N. chamelae* n. sp., is described from the Chamela-Cuixmala biosphere reserve in the Pacific coast of Jalisco, Mexico. This new species is placed within the subgenus *Harpoheterospilus* as it has an almost indistinct suture between the second and third metasomal terga and by the absence of a delineated apical area on the second metasomal tergite. *Neoheterospilus chamelae* is distinguished from the other species of the subgenus, *N. (H.) falcatus*, by its smooth vertex, single transverse carina in the prescutellar sulcus, a longer basal carina on the propodeum, and an elongate first metasomal tergite.

Resumen.—Se describe una nueva especie de *Neoheterospilus*, *N. chamelae* n. sp., de la reserva de la biósfera Chamela-Cuixmala en la costa del Pacífico en Jalisco, México. Esta nueva especie es incluida dentro del subgénero *Harpoheterospilus* por tener una sutura casi indistinguible entre el segundo y tercer tergos metasomales, y por la ausencia de un área apical delineada en el segundo tergo metasomal. *Neoheterospilus chamelae* se distingue de la otra especie del subgénero, *N. (H.) falcatus*, por presentar un vertex liso, una sola carina transversal en el surco prescutelar, y la carina basal en el propodeo y el primer tergo metasomal más largos.

The doryctine genus *Neoheterospilus* was erected by Belokobylskij (2006) to contain ten species, three of which were previously described and assigned to the megadiverse, polyphagous genus *Heterospilus* Haliday. *Neoheterospilus* was distinguished from the latter genus on the basis of a highly modified, unusually shaped ovipositor, and on the frequent presence of a basal area on the second metasomal tergite. This author also placed the genus in the tribe Heterospilini and divided it into two subgenera: *Neoheterospilus*, represented by nine species from the South Palaearctic and Old World tropics, and *Harpoheterospilus*, which included only one species, *N. falcatus* (Marsh), originally described from Venezuela and Brazil (Quicke and Marsh 1992).

Recent collecting trips carried out as part of an ongoing barcoding study of the doryctine fauna from the Chamela-Cuixmala Biosphere Reserve, in Jalisco, Mexico, have revealed the existence of an undescribed species of *Neoheterospilus*. Here we describe this new species, which represents the first record of the genus in Mexico and Mesoamerica. Preliminary molecular evidence has shown that *Neoheterospilus* may represent a derived lineage within *Heterospilus* (Zaldívar-Riverón et al., in prep.). However, we maintain the current status of this taxon until more evidence is gathered.

MATERIALS AND METHODS

Specimens assigned to *Neoheterospilus* were collected during three field trips to

the Chamela-Cuixmala Biosphere reserve carried out during June, September and November 2009, and February 2010. Four different collecting techniques were employed during these trips, though all specimens of the new species were collected either with light traps or sweep nets. All specimens were preserved in 100% ethanol and subsequently taken to the laboratory to obtain DNA sequence data for a barcoding study using a non-destructive DNA extraction technique. All specimens were air dried and mounted. Specimens are deposited in the Colección Nacional de Insectos (CNIN), Instituto de Biología, Universidad Nacional Autónoma de México, and in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN).

Association of males with the newly described species was confirmed by generating barcoding sequences for all specimens of both sexes. Sequence data for the specimens included in this study will be published elsewhere. Our description mostly follows Belokobyl's (2006) format in order to facilitate comparison of the new species with the described species of the genus. The terminology employed follows Sharkey and Wharton (1997), but Belokobyl's and Maeto's (2009) wing venation nomenclature is also included in parentheses. Photographs were taken and edited using a Leica® Z16 APO-A stereoscopic microscope, a Leica® DFC295/DFC290 HD camera, and the Leica Application Suite® program. All photographs were uploaded to the Morphbank web site (www.morphbank.org).

TAXONOMY

Neoheterospilus (*Harpoheterospilus*)

chamelae n. sp.

(Figs 1A–F, 2A–D)

Type material.—**Holotype**: ♀, Mexico, Jalisco, Chamela Biostation, UNAM, near lab, 19.49814 N-105.0444 W, 95 m, 23–24 June 2009, light trap,

tropical dry forest, Clebsch, Zaldívar-Riverón, Polaszek coll. **Paratypes**: 9♀, same data as holotype; 2♀ and 1♂, Mexico, Jalisco, Chamela Biostation, UNAM, camino Chachalaca, 19.49934 N-105.03833 W, 56 m, 25–27 June 2009, light trap, sweep net, tropical dry forest, Clebsch, Zaldívar-Riverón, Polaszek coll.; 1♂, Mexico, Jalisco, Chamela Biostation, UNAM, camino Chachalaca, 19.49785 N-105.04456 W, 120 m, 6 September 2009, sweep net, tropical dry forest, Clebsch, Zaldívar-Riverón coll.; 1♂, Mexico, Jalisco, Chamela Biostation, UNAM, camino Chachalaca, 19.49934 N-105. 105.03833 W, 56 m, 18 September 2009, sweep net, tropical dry forest, Zaldívar-Riverón coll.; 1♂, same data as holotype except date (24–25 June 2009); 1♂, Mexico, Jalisco, Chamela Biostation, UNAM, near lab, 19.49858-105.04417, 92 m, 19–20 November 2009, light trap, tropical dry forest, Zaldívar-Riverón coll.; 1♂, Mexico, Jalisco, Fundación Chamela-Cuixmala, Poza Jaguar, 19.42927 N-104.97968 W, 66 m, 5 September 2009, sweep net, tropical dry forest, H. Clebsch, A. Zaldívar-Riverón coll.; 3♀, Jalisco, Chamela Biostation, UNAM, camino Calandria (mirador), 19.50485 N-105.03786, 45 m, 24 February 2010, sweep net, tropical dry forest A. Zaldívar-Riverón, J. J. Martínez; 1♀, Jalisco, Chamela Biostation, UNAM, camino Chachalaca, 19.4997 N-105.03851 W, 51 m, 25 February 2010, light trap, tropical dry forest A. Zaldívar-Riverón, J. J. Martínez; 2♀, 1♂, Jalisco, Chamela Biostation, UNAM, near lab, 19.4986 N-105.04411 W, 20 February 2010, light trap, tropical dry forest A. Zaldívar-Riverón, J. J. Martínez; 1♀, 1♂, Jalisco, Chamela Biostation, UNAM, camino Buho, 19.49913 N-105.04217 W, 25 February 2010, Sweeping net, tropical dry forest A. Zaldívar-Riverón, J. J. Martínez.

Description.—**Female**: Body length 2.6–3.5 mm (Fig. 1A); fore wing length 2.0–2.4 mm.

Head: 1.6–2.0 times wider than median length. Occipital carina complete and joining hypostomal carina before mandible. Head behind eyes (dorsal view) roundly narrowed. Transverse diameter of eye 2.4–2.6 longer than temple (dorsal view). POL 0.7–1.0 times Od, 0.5–0.7 times OOL. Eye 1.2–1.3 times as high as broad. Malar space 0.2–0.3 times eye height, 0.6–0.8 times basal width of mandible. Face

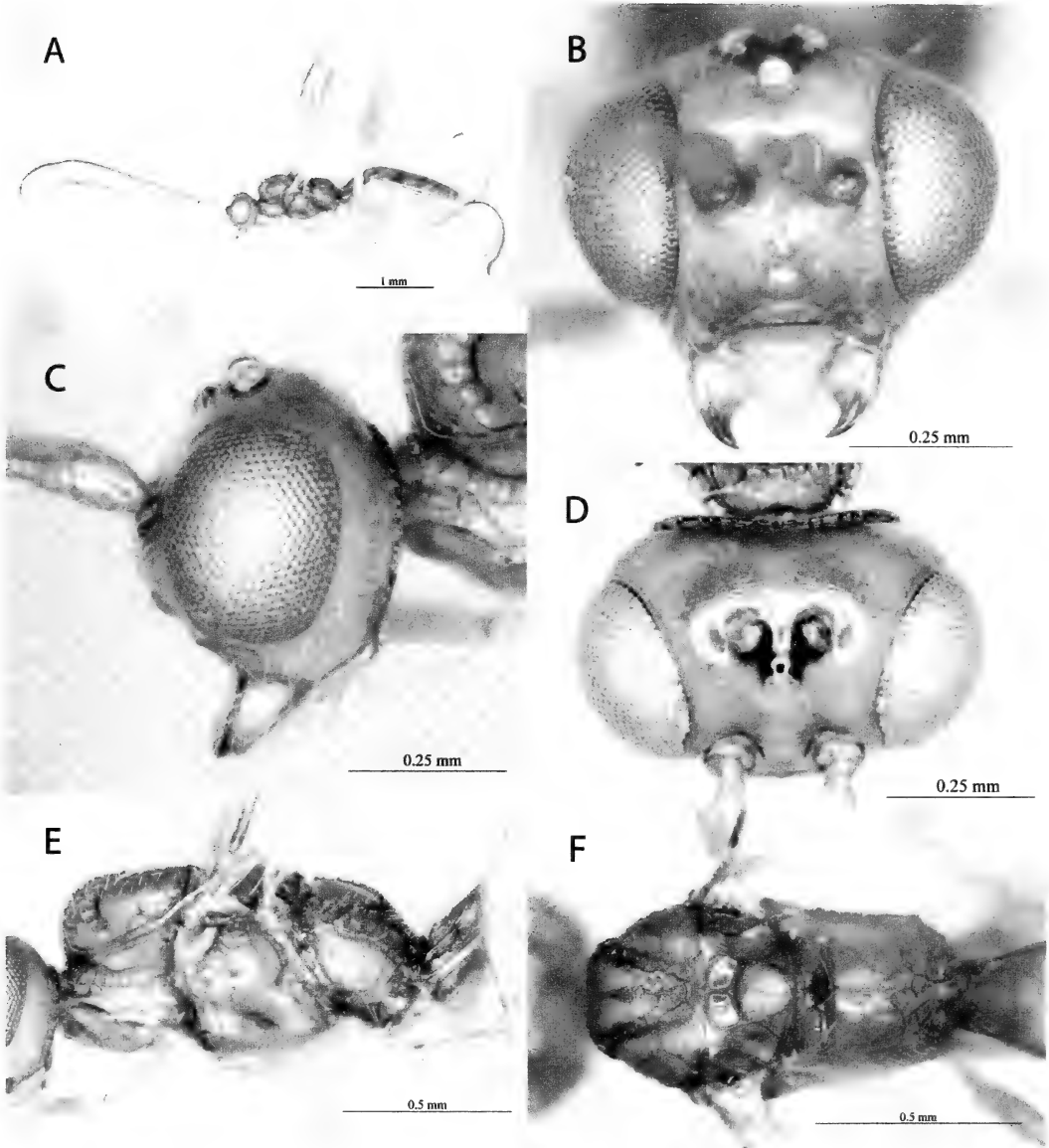


Fig. 1. *Neoheterospilus chamelae* n. sp.: A, habitus of female, lateral view; B, head, anterior view; C, head, lateral view; D, head, dorsal view; E, mesosoma, lateral view; F, mesosoma, dorsal view.

width 1.5–1.6 time eye height of face and clypeus combined. Width of hypoclypeal depression 1.6–1.8 times distance from edge of depression to eye, 0.3–0.4 times width of face. Antenna filiform, 24–25 antennomeres. Scapus 1.3–1.4 times as long as maximum width. First flagellomere 4.0–4.5 times longer than wide, 1.1–1.2 longer than second segment. Penultimate flagel-

lomere 0.4–0.5 times as long as wide, 0.6 times as long as first segment, as long as apical flagellomere.

Mesosoma (Figs 1E, F): 1.7–1.8 times longer than high, and 1.8–1.9 times longer than wide. Mesoscutum 0.7–0.8 times as long as wide. Median lobe of mesoscutum weakly convex anteriorly. Prescutellar depression with a single median carina, finely

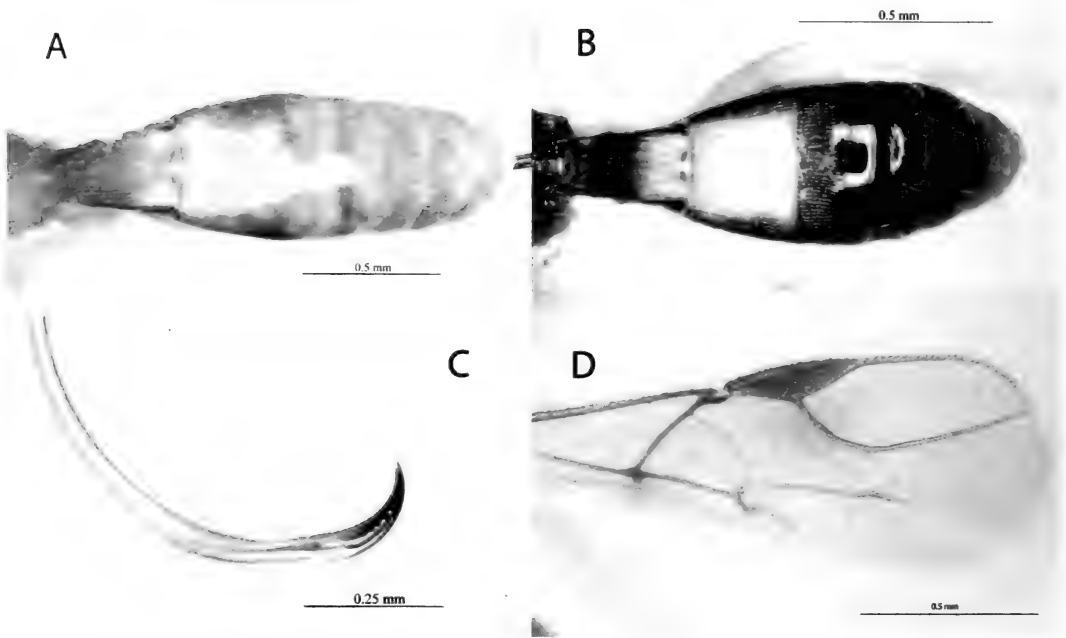


Fig. 2. *Neoheterospilus chamelae* n. sp.: A, metasoma of female, dorsal view; B, metasoma of male; C, apex of ovipositor; D, fore wing of female.

rugulose, 0.4–0.5 times as long as scutellum. Sternauli wide and scrobiculate.

Wings: fore wing 3.0–3.3 times longer than wide (Fig. 2D). Pterostigma 0.7–0.8 times as long as R (metacarpus). Vein r (first radial abscissa) 1.3–1.7 times as long as 3RSa (second radial abscissa), 0.3 times as long as 3RSb (third radial abscissa), and 0.5–0.6 times as long as trace of 2RS (first radiomedial vein). Vein (RS+M)a (first abscissa of medial vein) slightly curved. Discal (discoidal) cell 1.4–1.7 times longer than wide. Hind wing 5.0–5.2 times longer than wide. Vein SC+R (second abscissa of costal vein) absent. Vein M+CU (first abscissa of mediocubital vein) 0.7–0.8 times as long as 1M (second abscissa). Vein m-cu (recurrent vein) unsclerotised.

Legs: Hind coxa with distinct basoventral corner and without basoventral tooth. Hind femur 3.3–3.5 times longer than wide. Hind tibia 8.0–8.5 times longer than wide and 1.0–1.2 times longer than hind tarsus. Second segment of hind tarsus 0.6–0.7 times as long as basitarsus, 1.4–1.5

times as long as fifth segment (without pretarsus).

Metasoma: 1.1–1.2 times as long as head and mesosoma combined (Fig. 2A). First tergite slightly widened towards apex, 1.7–2.1 times longer than apical width; its basal sternal plate (acrosternite) 0.3 times as long as first tergite. Basal area of second tergite absent. Median length of second tergite 0.7–0.9 times its basal width, 1.1–1.3 times length of third tergite. Second suture shallow, almost indistinct. Ovipositor sheath 0.8–1.0 times as long as metasoma. Ovipositor thick, its apex sickle shaped (Fig. 2C). Ovipositor sheath distinctly and irregularly widened apically.

Sculpture and pubescence: Vertex smooth, occasionally with faint and poorly defined transversal striate sculpture (Fig. 1D); frons smooth (Figs 1B, D); face weakly acinose-coriaceous, turning smooth and slightly swollen medially (Fig. 1B); temple smooth (Fig. 1C). Pronotum coriaceous (Fig. 1E), pronotal furrow distinctly scrobiculate, mesoscutum strongly coriaceous, with rugose medioposterior area;

notauli complete and scrobiculate; scutellum coriaceous; prescutellar depression smooth to finely coriaceous, with a single median carina (Fig. 1F). Mesopleuron smooth medially, turning coriaceous posteriorly; subalar groove scrobiculate; sternaulus deep and scrobiculate (Fig. 1E). Metapleuron coriaceous, with two subvertical carinae posteriorly. Basolateral areas of propodeum coriaceous; remaining areas of propodeum strongly rugose-reticulate; areola delineated by carinae, with long median carina, 0.7–0.8 times as long as median length of scutellum (Fig. 1F). Hind coxa entirely coriaceous. Hind femur slightly coriaceous, turning smooth ventrally. First metasomal tergite longitudinally striate, with two more distinct anterior longitudinal carinae along anterior half of tergite; second tergite longitudinally striate, occasionally with weak granular sculpture between striae; remaining terga smooth (Fig. 2A). Head except eyes, mesoscutum, and pronotum covered by short, erect setae. Mesopleuron glabrous medially. Propodeum and metapleuron sparsely setose. Hind tibia with short semi-erect setae, more dense ventrally. Metasoma with first and second terga with sparsely and uniformly distributed short setae, remaining terga mostly glabrous, only with a transverse row of sparse setae subapically. Ovipositor sheath uniformly covered by long, erected setae.

Colour: Head, mesosoma and metasoma honey yellow (Fig. 1A); antennae honey yellow basally, gradually turning brown to the tip; ventral side of head, mouth parts, legs and ventral surface of metasoma pale yellow. Ovipositor sheath dark brown. Wings hyaline, veins light brown, pterostigma brown (Fig. 2D).

Male.—Body length 1.7–2.3 mm. Fore wing length 1.4–1.9 mm. Hind wing with brown to honey yellow sclerotised enlargement, length almost equal to distance from base of hind wing to base of enlargement. Similar to female except darker metasomal terga, with second and apical part of first

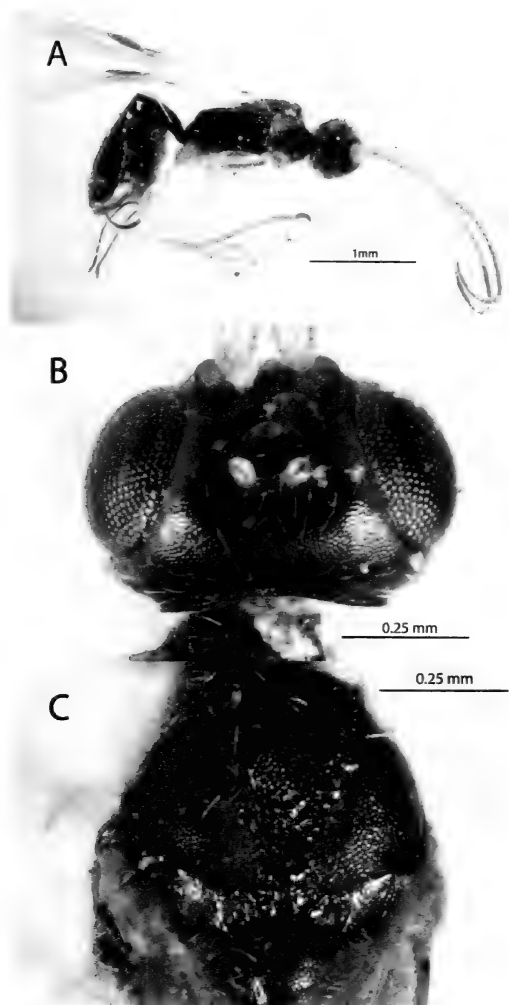


Fig. 3. *Neoheterospilus falcatus* (Marsh): A, habitus of female, lateral view; B, head, dorsal view; C, mesoscutum and anterior part of scutellum, dorsal view.

tergites pale yellow. Second tergite entirely and third in basal half striate. Antenna with 17–22 antennomeres. First metasomal tergite 1.5–1.7 times longer than apical width.

Remarks.—This species is similar to *N. (H.) falcatus*; however, it differs by having the body honey yellow (brown in *N. falcatus*; Fig. 3A), vertex usually smooth (coriaceous in *N. falcatus*; Fig. 3B), a single transverse carina in the prescutellar sulcus (three to five in *N. falcatus*; Fig. 3C), a longer basal carina on the propodeum (less than 0.7 times as long as median length of

scutellum in *N. falcatus*), and by an elongate first metasomal tergite (1.7–2.0 times longer than wide; 1.3–1.5 times in *N. falcatus*).

Neoheterospilus chamelae is included in the subgenus *Harpoheterospilus* by the almost indistinct suture between the second and third metasomal terga and the absence of a delineated apical area on second metasomal tergite. However, it differs from the original concept of the subgenus by having a single median carina in the prescutellar depression, and by usually having a smooth vertex.

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New records of *Encarsia* (Hymenoptera: Chalcidoidea: Aphelinidae) parasitising Aleyrodidae (Hemiptera: Sternorrhyncha) in Iran, with the description of a new species

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Abstract.—New records of aphelinids parasitizing several aleyrodid species in Iran are provided. *Encarsia alemansoori* Rasekh & Polaszek, n. sp., is described and illustrated. It is known so far from Iran only, and all known specimens were reared from the whitefly *Aleuroclava jasmini* (Takahashi). *Encarsia hamata* Huang & Polaszek is recorded for the first time from Iran, from the same host, and from *Aleurolobus marlatti* (Quaintance). *Encarsia hamata* is also recorded for the first time from Japan, from *Bemisia shinanoensis* Kuwana.

Encarsia species are mostly parasitoids of whiteflies and armoured scale insects (Diaspididae), and are of considerable economic importance. The systematics and biology of the genus are treated in detail by Heraty et al. (2008).

The purpose of this paper is to provide new records of *Encarsia* species, including a new species, reared from several aleyrodid species in Fars (Shiraz) Province in Iran. *Encarsia alemansoori* is clearly a member of the *Encarsia perflava*-group (see diagnosis below). It differs from all other known species of the *perflava*-group in the arrangement and structure of antennomeres 1–3 and their associated sensilla. The host, *Aleuroclava jasmini* (Takahashi) was described from the Oriental region (Taiwan, Takahashi 1932) and is now widespread throughout the tropics and subtropics, and thought to be established in parts of the New World where it has been introduced (Gill 1996). *Encarsia hamata* Huang & Polaszek is recorded for the first time outside China, from Iran and Japan.

Genomic DNA was successfully extracted from both species ($n=2$ *E. alemansoori*, $n=6$ *E.*

hamata) using a non-destructive protocol. Two males of *E. alemansoori* were prepared for examination with Scanning Electron Microscopy by gold coating; these specimens were later remounted on card rectangles.

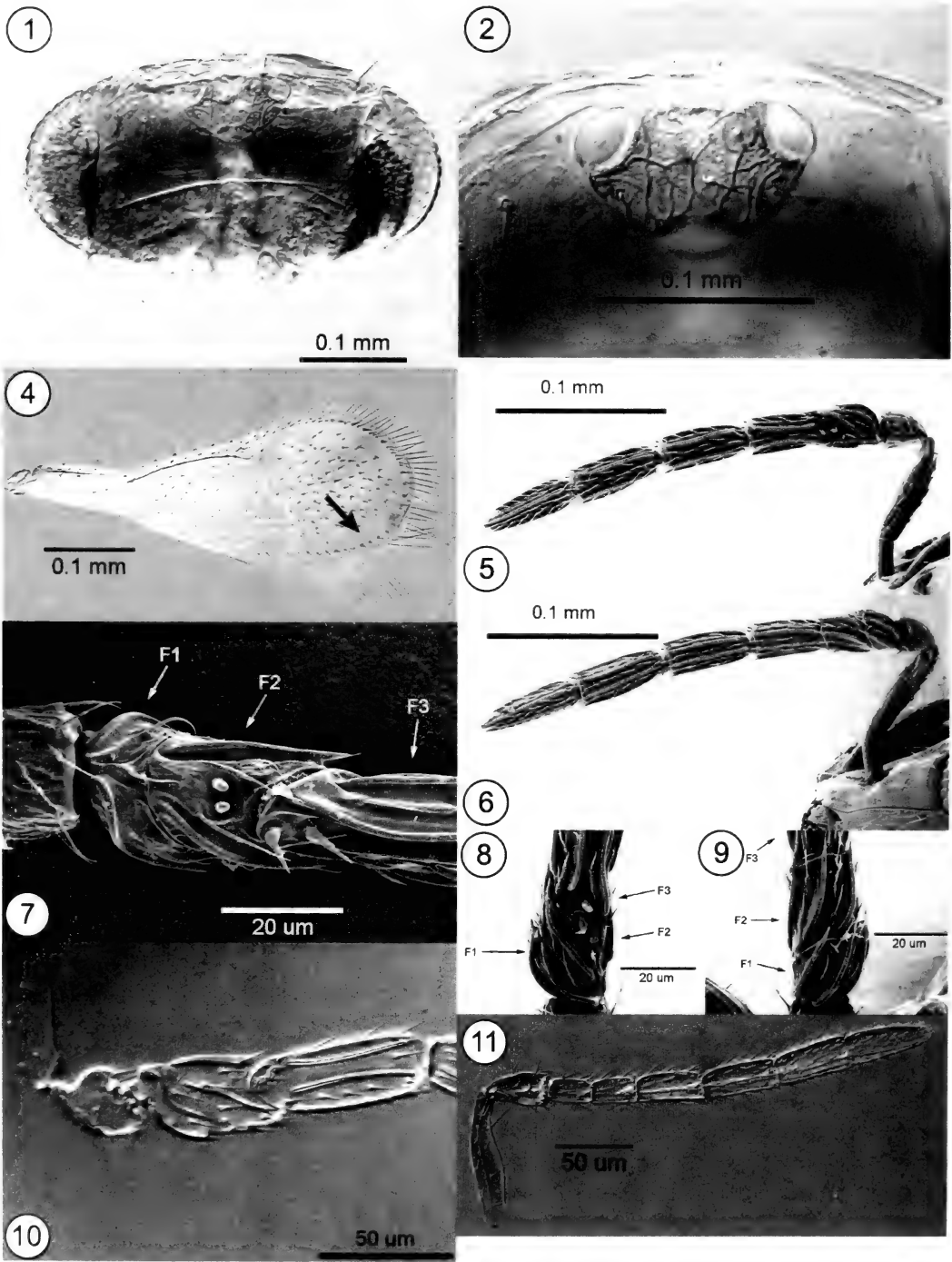
Abbreviations.—NHM: Natural History Museum, London, U.K., PPRII: Plant Protection Research Institute, Tehran, Iran

Encarsia perflava species-group – revised diagnosis

Both sexes.—Tarsal formula 5-5-5, fore wing without an obvious asetose area around stigmal vein, though often sparsely setose in posterior distal area (arrowed in Fig. 4). Scutellar sensilla widely spaced, separated by more than $2\times$ their diameter. Fore wing with marginal fringe relatively long, at least one third as long as maximum width. Emerging from Aleyrodidae.

Female.—Antenna with F1 and F2 approximately equal in length, clearly much shorter than remaining flagellomeres, and without longitudinal sensilla (Fig. 11).

Male.—Antenna with 6 flagellomeres; F1 and/or F2 and/or F3 always with specialised sensilla. These may be papillate,



Figs 1-2, 4-11. *Encarsia alemansoori* n. sp. 1-4, male holotype: 1, head; 2, stemmaticum; 4, fore wing; 5-9: male paratype: 5, antenna, inner aspect; 6, antenna, outer aspect; 7, 8, antenna, inner aspect, detail of F1-F3; 9, antenna, outer aspect, detail of F1-F3; 10, male holotype: antenna, inner aspect, detail of F1-F3 from slide-mount; 11, female paratype, antenna.

spiniform, ampulliform or pit sensilla (see Huang and Polaszek 1998, and Figs 5–10).

Currently included species: *ancistrocera*, *antiopa*, *bothrocera*, *?cappa*, *cibcensis duorunga*, *echinocera*, *farinaria* *?hamulata*, *justicia*, *leptosoma*, *notha*, *perflava*, *?picta*, *synaptocera*, *viggianii*.

***Encarsia alemansoori* Rasekh & Polaszek
n. sp.
(Figs 1–12)**

Description.—Male. **Colour:** Head yellow, the stemmaticum and occiput brown (Figs 1, 2). Meso- and metasoma (Fig. 2) largely brown (as in typical male *Encarsia*); posterior mid lobe, side lobes, scutellum and propodeum centrally, yellow. Antennae and legs uniformly yellow. Fore wings (Fig. 4) hyaline or very faintly infusate below marginal vein.

Morphology: Stemmaticum with irregular vermiculate/reticulate sculpture (Fig. 3). Antenna (Figs 5–10) with F1–F3 greatly modified; F2 bearing 2 papillate sensilla ventrally, F3 with 2 ampulliform sensilla ventrally (Figs 5, 7, 8, 10). Mid lobe of mesoscutum (Fig. 2) with 6 setae arranged symmetrically, side lobes with 2 setae each. Scutellar sensilla widely separated, by a distance of about 3.5× the width of a sensillum. Distance between anterior pair of scutellar setae slightly smaller than between posterior pair. Fore wing (Fig. 4) 2.7× as long as maximum width of disc. Marginal fringe 0.54× as long as width of disc. Submarginal vein with 2 setae, marginal vein anteriorly with 7 setae. Basal cell with 3 setae. Tarsal formula 5-5-5. Apical spur of mid tibia subequal in length to short side of corresponding basitarsus. Tergites laterally with the following numbers of setae: T1: 0, T2: 1, T3: 1, T4: 1, T5: 4, T6: 4, T7 with 4 setae.

Female.—Morphology as for male, except for antennal (Fig. 11) and genitalia characters (Fig. 12). Antennal formula 1,1,3,3. F1 and F2 subequal and short, without sensilla. F3 and F4 with 2, F5 and F6 with 3,



Fig. 3. *Encarsia alemansoori* n. sp., dorsal meso- and metasoma.

sensilla. Ovipositor (Fig. 12) 1.6× as long as mid tibia. Third valvulae apically rounded, 0.46× as long as second valvifers.

Species group placement.—*E. perflava* group.

Distribution.—Iran.

Host.—*Aleuroclava jasmini* (Takahashi).

Material examined.—Holotype ♂ (on slide), IRAN: Fars (Shiraz), Kazeroun 29°36'53"N 51°39'30"E Bahram Rasekh col. ex *Aleuroclava jasmini* on *Aegle correa* 15.v.2009 (PPRII). Paratypes 2♀ (on slides), same data as holotype, DNA528, 529 (NHM, PPRII). Paratype ♂ (gold-coated for SEM) IRAN: Fars (Shiraz), 29°36'N 52°31'52"E Bahram Rasekh col. ex *Aleuroclava jasmini* on *Citrus reticulata* × *C. limettioides* ("bakraei") 15.v.2009 (NHM). Paratypes (card-mounted) 12♀ IRAN: Fars (Shiraz), 29°36'N 52°31'52"E Bahram Rasekh col. ex *Aleuroclava jasmini* on *Citrus reticulata* × *C. limettioides* ("bakraei") 15.v.2009 (NHM, PPRII).

Comments.—*Encarsia alemansoori* is morphologically most similar to *E. bothrocera*

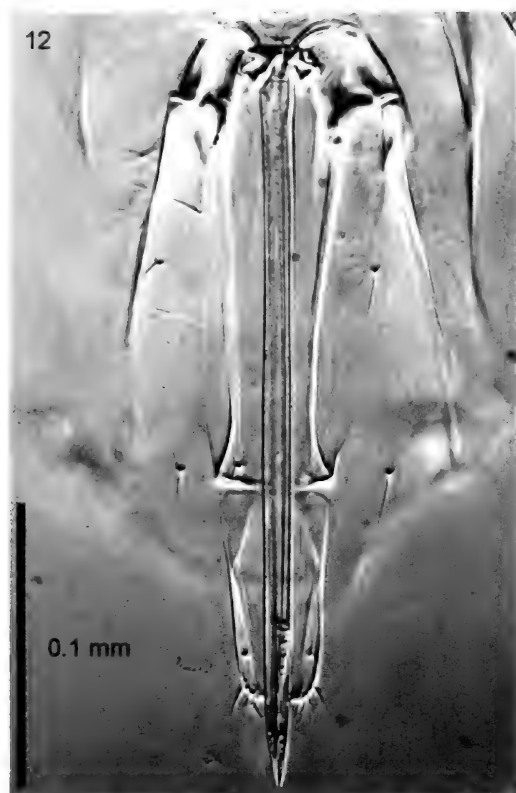


Fig. 12. *Encarsia alemansoori* n. sp., female paratype, ovipositor.

Huang & Polaszek, and *E. perflava* Hayat (Hayat, 1989; Huang and Polaszek, 1998). It can be distinguished from both these species by the following combination of characters: male: F1 without specialised sensilla; F2 with two papillate sensilla; F3 with two ampulliform sensilla (Figs 5–10); female: mid lobe of mesoscutum with 3 pairs of setae, side lobes each with 2 setae (mid lobe with 2 pairs, and side lobes with 3 setae in *E. bothrocera* and *E. perflava*). The females of all three species are otherwise very similar.

There has been a certain amount of confusion in the past concerning the *E. lahorensis* species-group established by Viggiani and Mazzone (1979), and the *perflava*-group established by Hayat (1989). Our current view is that the two groups are distinct, with *E. lahorensis* sharing very few of the diagnostic charac-

ters of the *perflava*-group. However, of the four species included in the group by Hayat (1989), only *E. perflava* and *E. leptosoma* appear to really belong there.

Encarsia hamata Huang & Polaszek

Encarsia hamata Huang & Polaszek, 1998: 1888–1890.

Several new distribution and host records are now known since the description of this species from China, as follows:

Distribution.—China, Iran, Japan.

Hosts.—*Aleuroclava jasmini* (Takahashi), *Aleurolobus marlatti* (Quaintance) (Iran); *Bemisia shinanoensis* Kuwana (Japan).

Material examined.—1♀ IRAN: Fars (Shiraz), Kazeroun 29°36'53"N 51°39'30"E Bahram Rasekh col. ex unknown whitefly on *Ziziphus spinachristi* 15.v.2009 (DNA522a) (NHM); 2♀ IRAN: Fars (Shiraz), 29°36'N 52°31'52"E Bahram Rasekh col. ex *Aleurolobus marlatti* on *Citrus aurantium* 5.v.2009 (DNA523a/ 525) (NHM; PPRII); IRAN: Fars (Shiraz), Kazeroun 29°36'53"N 51°39'30"E Bahram Rasekh col. ex *Aleuroclava jasmini* on *Aegle correa* 15.v.2009 (DNA526, 527) (NHM, PPRII); 4♀ IRAN: Fars (Shiraz), Kazeroun 29°36'N 52°31'52"E Bahram Rasekh col. ex *Aleuroclava jasmini* on *Citrus reticulata* × *C. limettoides* ("bakraei") 15.v.2009 (NHM, PPRII); 1♀ IRAN: Fars (Shiraz), 29°36'N 52°31'52"E Bahram Rasekh col. ex *Bemisia tabaci* on *Helianthus annuus* 15.v.2009 (DNA531) (NHM; PPRII); 1♀ JAPAN: Shizuoka Prefecture, Kosai City 34°43'6.48"N 137°31'53.85"E 28.i.1999 M. Ota. Ex *Bemisia shinanoensis* on *Spiraea cantonensis* (NHM).

ACKNOWLEDGMENTS

BR is grateful to his PhD supervisor Prof H. Alemansoor, after whom the new species is named, for guidance.

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Revision of the European, North-African and Central Asian species of the genus *Norbanus* Walker 1843 (Hymenoptera: Pteromalidae)

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Abstract.—The European, North-African and Central Asian species of the genus *Norbanus* Walker are revised, providing an illustrated key to males and females of all the species. Three new synonymies are proposed: *Norbanus globulariae* (Szelényi 1941) = *Norbanus giordanii* (Ferrière 1952), **n. syn.**; *Norbanus meridionalis* (Masi 1922) = *Norbanus mordellidarum* Dzhanokmen 1999, **n. syn.**; *Norbanus obscurus* (Masi 1922) = *Norbanus erdoesi* (Szelényi 1974), **n. syn.** Both sexes of *N. guyoni* are redescribed, and its type locality clarified. A new host record together with distributional data are given for nine out of ten valid species.

The genus *Norbanus* Walker 1843 (Pteromalidae: Pteromalinae) consists of 38 species distributed all over the world, 13 of which have been described from the West and Central Palaearctic (Noyes 2003), and includes some of the largest Pteromalinae species (Dzhanokmen 1999).

So far, the species of *Norbanus* are mainly known as parasitoids of Cephidae (Hymenoptera), Curculionidae (Coleoptera) and occasionally Lepidoptera (Bouček and Rasplus 1991, Dzhanokmen 1999, Noyes 2003), but very little is known about the biology of most of the species and for many of them the host is unknown. *Norbanus scabriculus* (Nees 1834), was released in Canada for biological control of *Cephus pygmeus* (L.), a pest of wheat (Bouček and Rasplus 1991).

Already Graham (1969), in his review of the West Palearctic species of Pteromalinae, stated that the European species of the genus needed revision. With *Arthrolysis* Förster 1856 and *Picroscytus* Thomson 1878 placed in synonymy with *Norbanus* by Peck (in Muesebeck et al. 1951), Graham (1969) lists in his work 5 species of *Norbanus*: *N. scabriculus*, *N. meridionalis* (Masi 1922), *N.*

giordanii (Ferrière 1952), *N. globulariae* Szelényi (1941), and *N. albicrus* (Masi 1934). The latter was later placed in synonymy with *Cyrtotypus latipes* (Rondani 1874) (Pteromalidae) by Bouček (1974). However, Graham (1969) gives a key to females of only two *Norbanus* species, feeling uncertain as to the validity of the other species.

Five more *Norbanus* species were listed by the same author as *Picroscytoides* Masi 1922 (which was later placed in synonymy with *Norbanus* by Bouček (1990)): *N. cerasiops* (Masi 1922), *N. obscurus* (Masi 1922) and three unidentified species. He omitted *N. guyoni* (Giraud 1869), mentioned by Szelényi (1941) as *Arthrolysis guyoni*, and *N. calabrus* (Masi 1942), which Masi described as *Picroscytus calabrus*.

Later, Bouček (1969) described *N. laevis* and *N. albiventris* (as *Picroscytoides*), the latter being placed in synonymy with *N. calabrus* by Bouček (1990). Szelényi (1974) described *N. brevicornis* and *N. erdoesi* (the latter as *Picroscytoides*), and Bouček (1970) *N. tenuicornis*.

Then, Dzhanokmen (1999) in her review of the Kazakhstan species of *Norbanus*, separated two subgenera, *Norbanus* and

Picroscytoides, and mentions seven species, one of which being new: *N. (N.) mordellidarum* Dzhanokmen. Also, she provides a key to females and males of these species.

Thus, before this study, a comprehensive key to all the 13 species of *Norbanus* known in Europe, North Africa and Central Asia was lacking. Here we provide a revision of the genus and an illustrated key to males and females of all the valid species. Palearctic species of the genus comprise three more taxa, that we had not the opportunity to include in this study and will take into consideration in a further paper: *N. aiolomorphi* Yang and Wang 1993 and *N. arcuatus* Xiao and Huang 2001 from mainland China (Yang et al. 1993; Xiao and Huang 2001), and *N. ruschkae* (Masi 1927) from Taiwan.

MATERIAL AND METHODS

For the present revision we studied specimens of *Norbanus* from five European museums (whenever possible their types) and from the field. The examined material is deposited in the following institutions:

- GNHCM Genoa Natural History Civic Museum "G. Doria", Genoa, Italy;
- HNHM Hungarian Natural History Museum, Budapest, Hungary;

- MICO Mitroiu collection, Faculty of Biology, Alexandru Ioan Cuza University, Iași, Romania;
- MNHV Museum of Natural History of Venice, Venezia, Italy;
- NHM Natural History Museum, London, UK;
- NHMV Natural History Museum, Vienna, Austria.

Norbanus Walker 1843

The genus *Norbanus* belongs to the group of Pteromalinae genera bearing two spurs on the hind tibia, and differs from *Merisus* Walker 1835 and *Homoporus* Thomson 1878 in having a prepectus smaller than the tegula (Graham 1969; Bouček and Raspluš 1991). The very similar *Anorbanus* Bouček 1990 should differ from *Norbanus* mainly by the rounded antennal clava (Bouček 1990).

In this study we maintained the subgeneric division proposed by Dzhanokmen (1999), even if the only diagnostic character which separates the two subgenera is the hind margin of the first tergite, near straight in subgenus *Norbanus* s. str. and three-lobed in subgenus *Picroscytoides* Masi.

KEY TO FEMALES

- 1 Hind margin of first tergite straight or slightly convex in posterior part (Fig. 1) (subgenus *Norbanus* s. str.) 2
- Hind margin of first tergite three-lobed (Fig. 2) (subgenus *Picroscytoides*) 6
- 2 (1) Forewing with basal cell completely bare; postmarginal vein much shorter than marginal vein (Fig. 3); rather minute species (usually less than 2 mm). *N. tenuicornis* Bouček
- Forewing with basal cell either bare with only basal vein pilose or moderately to extensively pilose; postmarginal vein at least as long as (but often clearly longer than) marginal vein (Fig. 5); more robust species 3
- 3 (2) Basal cell uniformly hairy (Fig. 4); antennal club before spicula either gradually becoming pointed or globose 4
- Basal cell completely bare or at most pilose in its distal half (Fig. 5, 6); antennal club before spicula always gradually becoming pointed, never globose 5
- 4 (3) Speculum present; antenna slender with all segments longer than wide, gradually becoming shorter towards antennal apex; club two-segmented, globose, ending

- with a thin spicula (Fig. 22); head transverse in dorsal view (Fig. 13)..... *N. meridionalis* (Masi)
- Speculum absent; antenna short, thickening towards apex, with segments from 3rd to 6th subquadrate; club in appearance unisegmented with segments fused; club pointed bearing a short stocky spicula (Fig. 19); head globose in dorsal view with large rounded temples (Fig. 7) *N. brevicornis* Szélnyi
- 5 (3) Basal cell: few setae present on the basal vein and sometimes near it (Fig. 5); head strongly transverse in dorsal view, with eyes in lateral position and temples receding, $POL \leq OOL$ (Fig. 9) *N. scabriculus* (Nees)
- Basal cell hairy on the entire distal half (Fig. 6); head transverse but temples present and eyes in antero-lateral position; $POL \geq OOL$ (Fig. 10)..... *N. globulariae* (Szélnyi)
- 6 (1) Gaster very long and narrow, more than 4 times as long as broad and about twice as long as head plus mesosoma together, orange with distal third black; very large species (more than 10 mm) *N. guyoni* (Giraud)
- Gaster much shorter and broader, at most about 3 times as long as broad and not much longer than head plus mesosoma together (Fig. 8), with at most its basal half orange; smaller species (up to 7 mm but usually less) 7
- 7 (6) Gena with strongly developed quadrangular lamina at base of mandible (Fig. 16) *N. calabrus* (Masi)
- Gena with at most slightly developed rounded lamina at base of mandible (Fig. 15) . 8
- 8 (7) Sculpture of head and mesosoma very shallow, effaced *N. laevis* (Bouček)
- Sculpture of head and mesosoma deep, not effaced 9
- 9 (8) Antenna with clear spicula (Fig. 20), yellowish, darker towards pedicellus, proximal part of flagellum hardly as broad as pedicellus; head about 1.9 as broad as long in dorsal view and slightly higher than wide in frontal view; head and mesosoma from coppery-green to blackish, eyes brownish; gaster brownish, always without any reddish-orange part *N. obscurus* (Masi)
- Antenna without clear spicula (cf. Fig. 17), dark, proximal part of flagellum broader than pedicellus; head about 2.1–2.2 as broad as long in dorsal view and slightly wider than high in frontal view; head bluish-black, mesosoma bluish, eyes reddish; gaster at most with basal half orange *N. cerasiops* (Masi)
-

KEY TO KNOWN MALES

(characteristics that are not illustrated are similar to females)

- 1 Hind margin of first tergite straight or slightly convex in posterior part..... (subgenus *Norbanus* s. str.) 2
- Hind margin of first tergite three-lobed (subgenus *Picroscytoides*) 6
- 2 (1) Basal cell uniformly hairy; antennae either with pedicellate funicular segments with whorls of setae (Fig. 18) or with wider segments, covered by very dense short setae (Figs 17, 21) 3
- Basal cell completely bare or at most pilose in its distal half; antenna always with pedicellate funicular segments with whorls of setae 4
- 3 (2) Speculum present; head transverse in dorsal view (Fig. 11); antenna with pedicellate funicular segments with whorls of setae (Fig. 18) *N. meridionalis* (Masi)
- Speculum absent; head globose in dorsal view with large rounded temples; antenna with wider segments, covered by very dense short setae. *N. brevicornis* Szélnyi

- 4 (2) Basal cell: few setae present on the basal vein and sometimes near it; head strongly transverse in dorsal view, with eyes in lateral position and temples receding, $POL \leq OOL$ *N. scabriculus* (Nees)
- Basal cell hairy on the entire distal half; head transverse, but temples present and eyes in antero-lateral position; $POL \geq OOL$ *N. globulariae* (Szelényi)
- 6 (1) Gaster mostly orange; antenna with pedicellate funicular segments with whorls of setae 7
- Gaster blackish, at most slightly paler basally; antenna with wide segments, covered by very dense short setae 8
- 7 (6) Base of gaster, next to petiole, orange, only tip black; antenna shorter, pedicellus plus flagellum only about 1.2 times as long as width of head; tibia entirely yellow ...
..... *N. guyoni* (Giraud)
- Both base and tip of gaster black; antenna longer, pedicellus plus flagellum 1.5 times as long as width of head; tibia infuscated medially *N. calabrus* (Masi)
- 8 (6) Antenna with pedicellus plus flagellum shorter than head width; head about 2.1–2.2 as broad as long in dorsal view (Fig. 12); head bluish-black, mesosoma bluish, eyes reddish *N. cerasiops* (Masi)
- Antenna with pedicellus plus flagellum longer than head width (Fig. 21); head about 1.9 as broad as long in dorsal view (Fig. 14); head and mesosoma dark green, eyes brownish *N. obscurus* (Masi)

Subgenus *Norbanus* s. str.

Norbanus (*Norbanus*) *brevicornis* Szelényi (Figs 7, 19)

Norbanus brevicornis Szelényi, 1974.

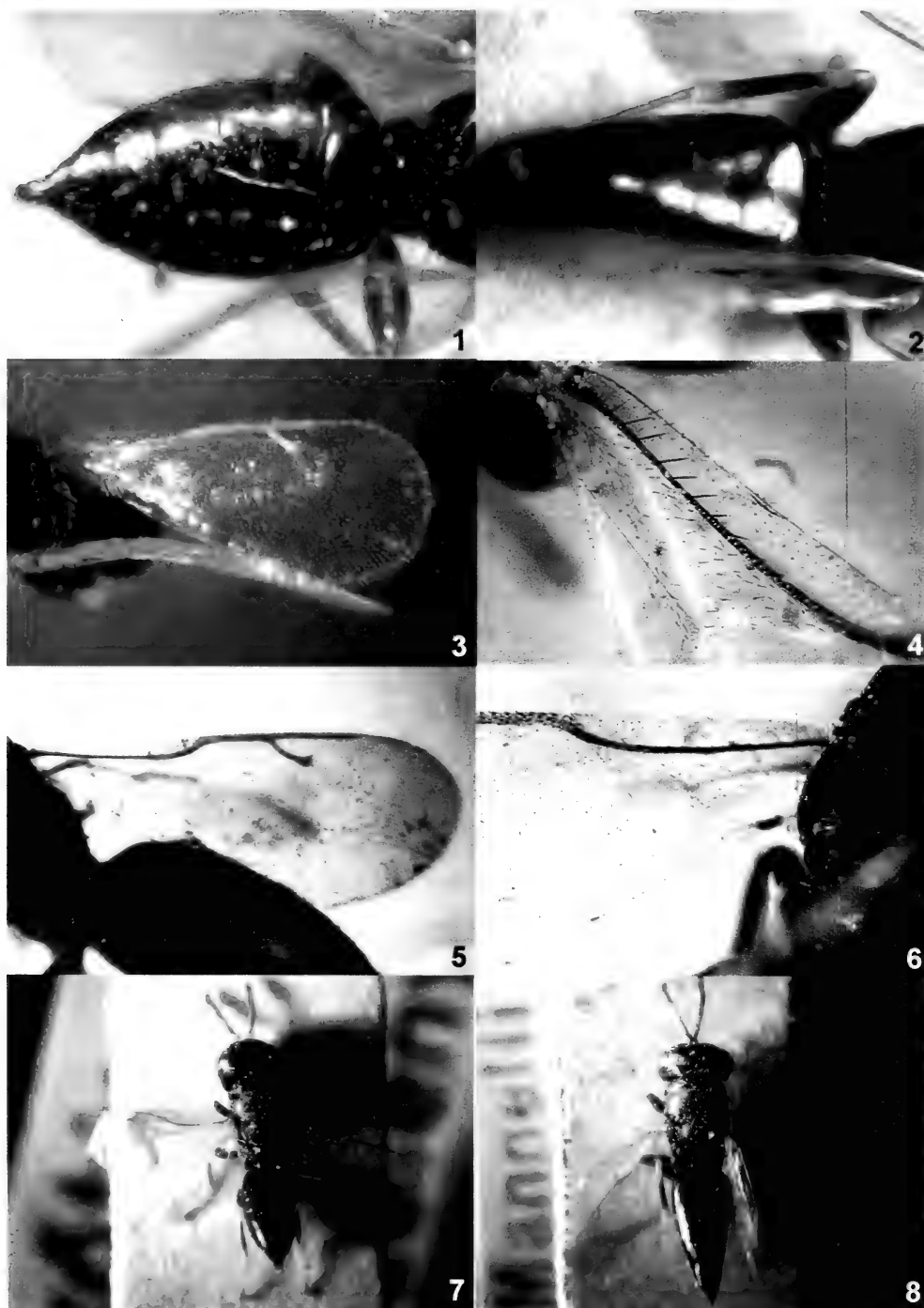
Diagnosis.—The species can be easily distinguished from all the other species of *Norbanus* by its large, globose head with large rounded temples, short antennae and entirely pilose fore wings (cf. Figs 7, 19); in males, the antennae are covered with very dense short setae.

Distribution.—Hungary (Szelényi 1974). Previously unrecorded for Croatia, Greece, France and Romania.

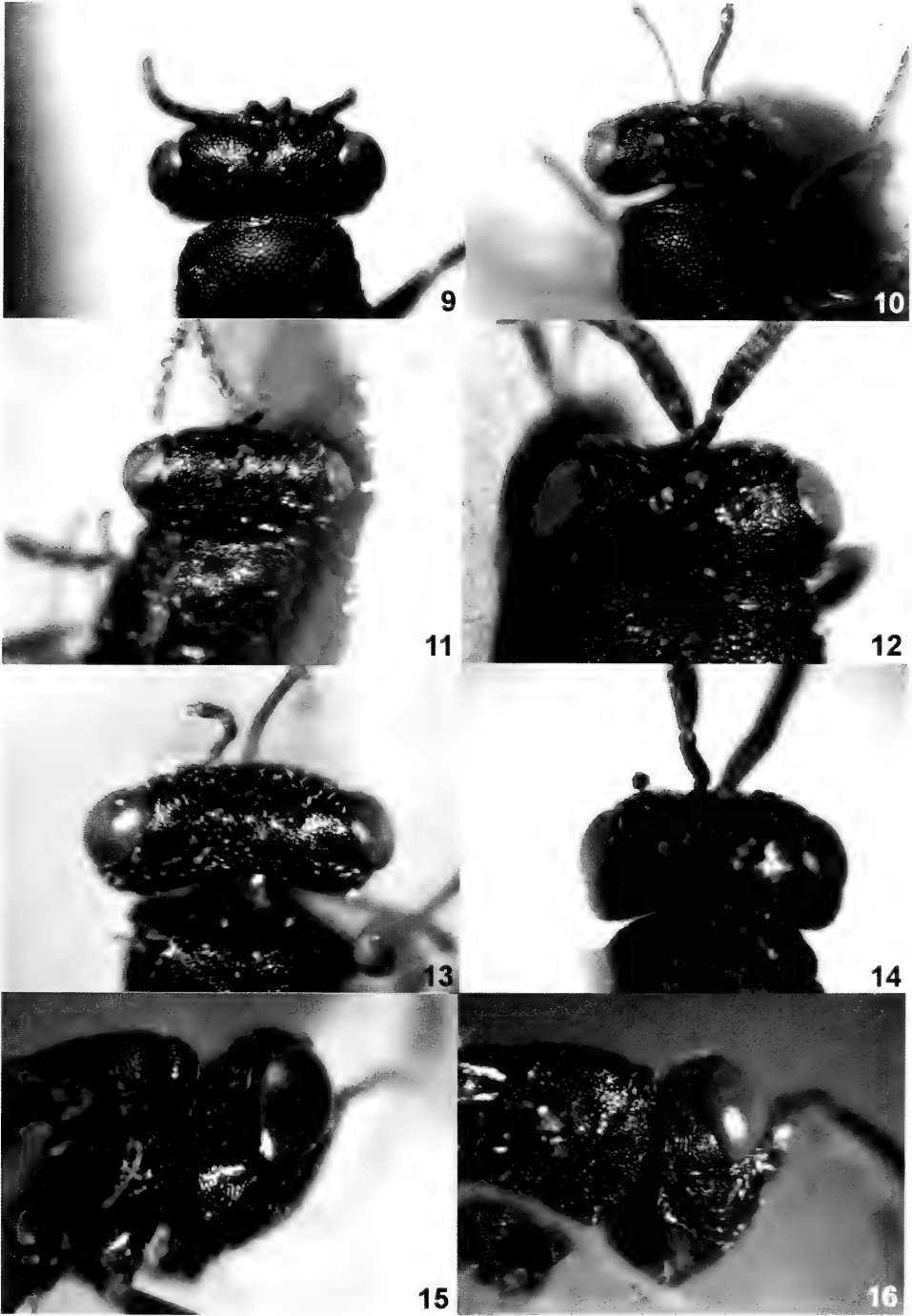
Biology.—Unknown.

Material examined.—**Type material:** HNHN: 1♀ 'Mezőtúr, 20.VIII.1966, leg. Szelényi', '10484', '*Norbanus brevicornis* sp. n. det. Dr. Szelényi 1', '*Holotypus Norbanus brevicornis* Szelényi', 'Hym. Typ. No. 4253 Mus. Budapest'. **Additional material:** NHM: 1♂ '*Picroscytoides obscurus* Masi, det. Z. Bouček 1987', 'Jugoslavia, Jadran Biograd n/m Bouček 11.VII.1965'; 1♂ '*Picroscytoides obscurus* Masi, det. Z. Bouček 1980', 'Greece, Pelop. Olympia, 6.VII.79 M.C. Day'. The following specimens are part of Graham's collection, bearing the same registra-

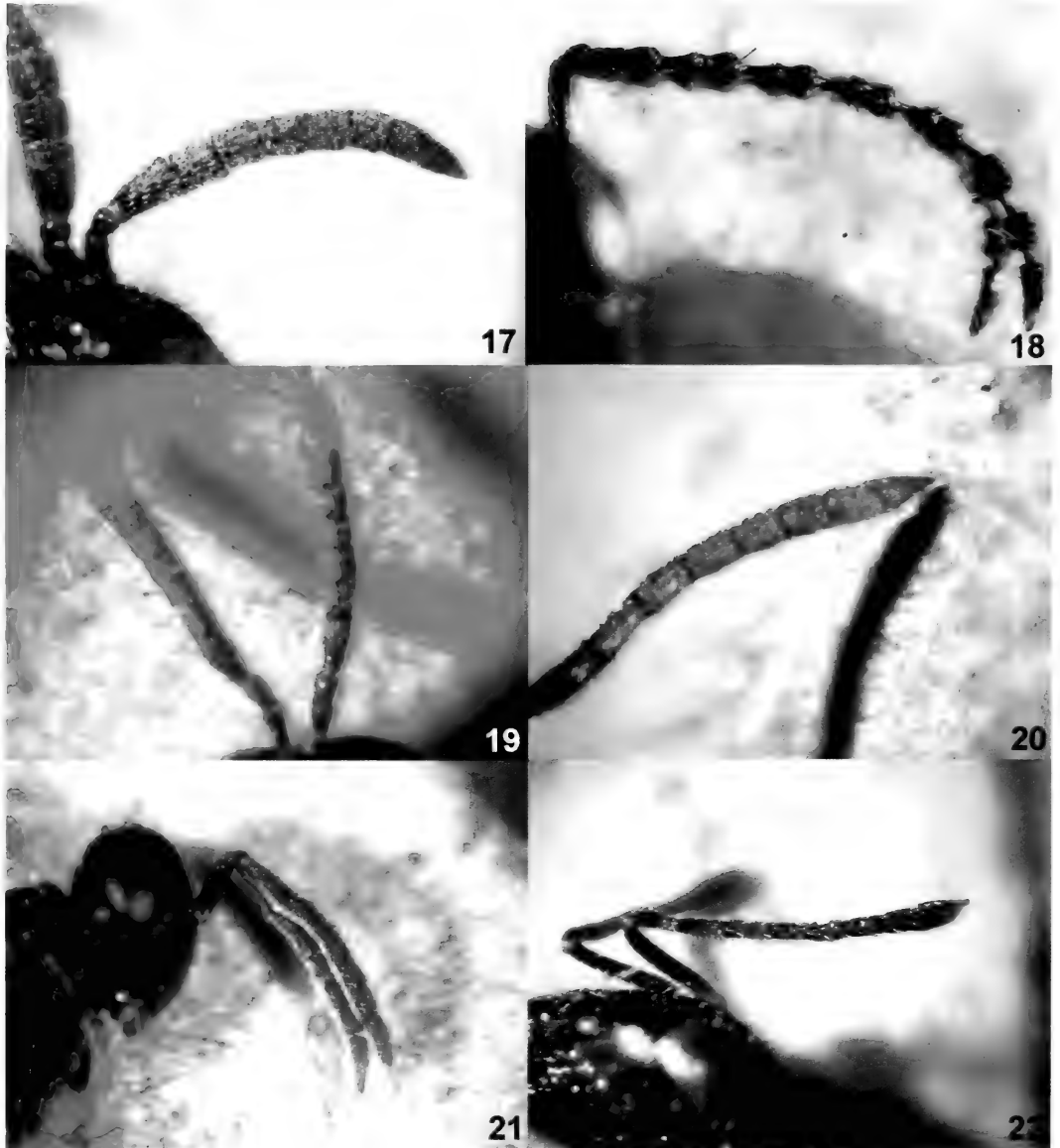
tion label: 'M. W. R. de V. Graham coll., BMNH(E) 1995-489' (exceptions indicated): 1♀ '*Norbanus brevicornis* Szel.', 'France: Vaucluse nr. Bédoin, 9.VII.1983; 1♀ same locality, 23.VI.1986; 1♀ same locality, 28.VI.1985; 1♀ same locality, 29.VII.1979; 1♀ same locality, 29.V.1985; 1♀ same locality, 28.V.1982; 1♀ same locality, 28.VI.1986; 1♀ same locality, 15.VII.1981; 1♀ same locality, 11.VII.1980; 1♂ '*brevicornis* subgen. *Masioscytus* Masi', 'France: Vaucluse nr. Bédoin, 21.V.1982; 1♂ same locality, 18.VII.1980, Les Constants; 1♂ same locality, 8.VII.1986; 1♂ same locality, 25.V.1982; 2♂ same locality, 22.VII.1981; 1♂ same locality, 3.VI.1985; 1♂ same locality, 10.VI.1985; 1♂ same locality, 15.VII.1981; 1♂ 'France, Vaucluse, Roussillon, 22.VI.1977' (no registration label); 1♂ 'Fme de Buar nr. Sault 10.VIII.79', 'France, Vaucluse, M. de V. Graham', 'M. de V. Graham BMNH 1983-2'; 2♂ 'France: Drôme, Col de Macuègne, 7.VIII.1975'; 1♂ 'France, B du Rhone, Fonscolombe, 10.VIII.1983'; 1♂ 'France: Dordogne Sarlat distr., nr. St. André d'Allas, 3.VIII.1974'. **MICO:** 1♀ '*Norbanus brevicornis* Szel. ♀, det. M. Mitroiu 2008', 'Greece, Kerkini, 20–26.VI.06 Malaise trap / N = 41°08'15.6; E = 023°13'01.2, Gordon Ramel leg.'; 2♀ '*Norbanus brevicornis* Szel. ♀, det. M. Mitroiu 2008', 'Romania, IS, Rez. Nat. Valea lui David 31.VII.1999, M.-D. Mitroiu leg.'



Figs 1-8. 1. *N. scabriculus* hind margin of the first tergite straight, ♀; 2. *N. calabrus* hind margin of the first tergite three-lobed, ♀ holotype; 3. *N. tenuicornis* postmarginal vein much shorter than marginal vein, ♀; 4. *N. meridionalis* basal cell uniformly hairy, ♀ paralectotype; 5. *N. scabriculus* basal cell completely bare and postmarginal vein longer than marginal vein, ♀; 6. *N. globulariae* basal cell pilose in its distal half, ♀; 7. *N. brevicornis* habitus showing the head globose in dorsal view, ♀ holotype; 8. *N. calabrus* habitus, ♀ holotype.



Figs 9–16. 9. *N. scabriculus* head in dorsal view, ♀; 10. *N. globulariae* head in dorsal view, ♀ holotype; 11. *N. meridionalis* head transverse in dorsal view, ♂ paralectotype; 12. *N. cerasiops* head in dorsal view, ♂ syntype; 13. *N. meridionalis* head transverse in dorsal view, ♀; 14. *N. obscurus* head in dorsal view, ♂ paralectotype; 15. *N. obscurus* gena with rounded lamina, ♀ paralectotype; 16. *N. calabrus* gena with quadrangular lamina, ♀ holotype.



Figs 17–22. 17. *N. cerasiops* antenna ending without a clear spicula, ♂ syntype; 18. *N. meridionalis* antenna, ♂ paralectotype; 19. *N. brevicornis* antennae, ♀ holotype; 20. *N. obscurus* antenna ending with a spicula, ♀ paralectotype; 21. *N. obscurus* antennae, ♂ paralectotype; 22. *N. meridionalis* antenna with a two-segmented globose club, ♀ paralectotype.

***Norbanus (Norbanus) globulariae*
(Szelényi)
(Figs 6, 10)**

Picroscytus globulariae Szelényi 1941.

Norbanus globulariae (Szelényi 1941), Graham (1969).

Picroscytus giordanii Ferrière 1952.

Norbanus giordanii (Ferrière), Graham (1969);
n. syn.

New synonymy.—In his description of *Picroscytus giordanii*, Ferrière (1952) compares his species with both *Norbanus* (= *Picroscytus*) *meridionalis* (Masi 1922) and *Norbanus* (= *Picroscytus*) *globulariae*. He

didn't see Szelényi's type material but mainly refers to proportions between marginal, postmarginal and stigmal veins given for both the other two species by Szelényi (1941) himself. Ferrière thought that his species had the postmarginal vein proportionally shorter than the others, and also lists some colour differences in antennae and hind tibiae. Studying type material of both *N. globulariae* and *N. giordanii* we found overlapping proportions in fore wing venation and that other differences are inconsistent. Thus, *N. giordanii* is considered a junior synonym of *N. globulariae*.

Diagnosis.—The species is very close to *N. scabriculus* (Nees), from which it differs mainly in having the basal cell hairy on the entire distal half (cf. Fig. 6).

Distribution.—Hungary, Italy (Szelényi 1941, Ferrière 1952). Previously unrecorded for France and Romania.

Biology.—The species was reared as a primary parasitoid of *Stigmatophora albiapicella* H. S. (Lepidoptera: Momphidae) from flower heads of *Globularia willkommii* Nym. (Graham 1969; Herting 1975). It also appears to be associated with flower heads of *Centaurea scabiosa* L., as one of the records below shows.

Material examined.—**Type material:** **HNHM:** 1♀ 'Budapest 1937 III/22 dr. Szelényi', 'E floribus Globulariae Willkommii', 'Picroscytus globulariae n. sp. Det. Szelényi', 'Typus', 'Cotypus Picroscytus globulariae Szel.', 'Hym. Typ. No. 2523 Mus. Budapest', Hungarian Natural History Museum Budapest'. **MNHV:** 1♀ '1709 Laguna veneta', 'Ricerche lagunari 1944-48', 'Staz. terr. N. 350', 'Giordani Soika', 'Picroscytus', 'giordanii sp. n. ♀', 'Cotype Ferrière', 'Paratypus'; 1♂ '1710 Laguna veneta', 'Ricerche lagunari 1944-48', 'Staz. terr. N. 168', 'Giordani Soika', 'Picroscytus', 'giordanii sp. n. ♂', 'Cotype Ferrière', 'Paratypus'; 1♂ '1711 Laguna veneta', 'Ricerche lagunari 1944-48', 'Staz. terr. N. 455', 'Giordani Soika', 'Picroscytus', 'giordanii sp. n. ♂', 'Cotype Ferrière', 'Paratypus'. **Additional material:** **NHM:** 1♀ 'globulariae (Szel.)', 'France: Drôme, Col de Macuègne, ex Cent. scabiosa head em. 16.IX.1989', 'M. W. R. de V. Graham coll., BMNH(E) 1995-489'. **MICO:**

1♀ 'Norbanus globulariae (Szel.) ♀, det. M. Mitroiu 08', 'Romania, CT, R.N. Valul lui Traian, 16.V.2007, leg. L. Fusu'.

***Norbanus (Norbanus) meridionalis* (Masi)**
(Figs 4, 11, 13, 18, 22)

Picroscytus meridionalis Masi 1922.

Norbanus meridionalis (Masi 1922), Graham (1969).

Norbanus (Norbanus) mordellidarum Dzhanokmen 1999; n. syn.

New synonymy.—Dzhanokmen (1999) described her *N. (N.) mordellidarum* mainly on the base of its characteristic fore wing venation and antennae (hairy basal cell, presence of speculum and bisegmented globose club), which well separated her species from both *N. (Norbanus) scabriculus* (Nees) and *N. (N.) brevicornis*. However, Dzhanokmen did not know Masi's paper, nor had she seen *N. (N.) meridionalis* type material. Our comparison of type material of *N. (N.) mordellidarum* and *N. (N.) meridionalis* showed that they are the same species, thus the former becomes a junior synonym of the latter.

Diagnosis.—The species can be distinguished from the other species of the genus by the fore wings with uniformly hairy basal cell and distinct speculum (cf. Fig. 4), thin antennae with long segments and the club being globose before the spicula, and transverse head (cf. Figs 11, 13, 22); in males the antennae have pedicellate funicular segments, with whorls of setae (cf. Fig. 18).

Distribution.—Hungary, Italy, Kazakhstan, Slovakia, Spain, Sweden (Noyes 2003). Previously unrecorded for Cyprus, France and Romania.

Biology.—The species was recorded from *Cephus pygmeus* (L.) (Hymenoptera: Cephidae) (Zhasanov 1986) and from some unknown Mordellidae (Coleoptera) on *Silene odoratissima* Bge. (Dzhanokmen 1999).

Material examined.—**Type material.** **GNHCM:** 1♀, 1 ♂ 'Paralectotype', 'Paralectotypus Picros-

cytus meridionalis Masi, 1922 Bouček det. 1970', 'CoTypus', 'Is. Giglio, VII.1902, G. Doria', 'Museo Civico di Genova'; 7♀ 'Paralectotype', 'PLT ♀ Picroscytus meridionalis Masi Det. Z. Bouček 1990', same locality and data. **NHM**: 'S-E Kazakhstan, S Taukumov, Dzhankmen 21.V.77 / from Mordellidae on *Silene odoratissima* Bge' [in Russian], 'HOLOTYPE ♀ *Norbanus mordellidarum* Dzhankmen', 'NHM(E) 1999-194', 'B.M. TYPE HYM 5.4114'. **Additional material**. **NHM**: 1♂ 'Norbanus meridionalis Masi', 'Cyprus: Limassol., 23.V.1934, G. A. Mavromoustakis, BM 1935-55', 'British Museum Loan No. 7214'. The following specimens are part of Graham's collection bearing the same registration label: 'M. W. R. de V. Graham coll., BMNH(E) 1995-489': 1♀ '? meridionalis M.', 'France: Vaucluse N. of Saumane, Grange Neuve, 16.VII.1981'; 1♀ 'near meridionalis Masi', 'France: B. du Rhone Nr. Rognes, 16.VII.1979'; 1♀ 'France: Drôme, Col de Macuègne, 21.VIII.1986'; 1♀ 'France: Drôme, La Poët-en-Percip, 24.VII.1994'. **NHNV**: 1♀ 'Is. Giglio, VII.1901', 'Arthrolisis scabricula (Nees) det. Masi'. **MICO**: 1♀ 'Norbanus meridionalis (M.) ♀, det. M. Mitroiu 2008', 'Rez. Agigea, 21.VI.2000, leg. L. Fusu'; 1♀ 'Norbanus meridionalis (M.) ♀, det. M. Mitroiu 2008', 'Romania: P.N. Măcin, fânaț, capc. Malaise, 23-25.VII.04'; 2♂ 'Norbanus meridionalis (M.) ♂, det. M. Mitroiu 2008', 'RO, CT, R.N. Canaraua Fetii, 16.V.2005, leg. Fusu, Popovici'.

Norbanus (Norbanus) scabriculus (Nees)
(Figs 1, 5, 9)

Pteromalus scabriculus Nees 1834.

Arthrolisis scabricula (Nees 1834), Giraud (1870).

Dimachus (Picroscytus) scabriculus (Nees 1834), Thomson (1878).

Picroscytus scabriculus (Nees 1834), Masi (1922).

Norbanus scabriculus (Nees 1834), Peck (1963).

Norbanus (Norbanus) scabriculus (Nees 1834), Dzhankmen (1999).

Diagnosis.—The species is characterized by a glabrous or almost glabrous basal cell, with a few setae present on the basal vein, occasionally a few more near it (cf. Fig. 5), thin antennae with club gradually becoming pointed, and strongly transverse head (cf. Fig. 9); in males the antennae have

pedicellate funicular segments bearing whorls of setae.

Distribution.—Azerbaijan, Canada, Croatia, Czech Republic, Germany, Hungary, Italy, Kazakhstan, Montenegro, Netherlands, Republic of Moldavia, Romania, Russia, Slovakia, Spain, Sweden, Ukraine (Noyes 2003). Previously unrecorded for Austria, France, Slovenia and United Kingdom (England).

Biology.—According to references traced via Noyes (2003), the species has been recorded as a primary parasitoid from *Agapanthia violacea* (F.) (Coleoptera: Cerambycidae), *Lixus juncii* Boh. (Coleoptera: Curculionidae), *Cephus pygmeus* (L.) (Hymenoptera: Cephidae) and *Trachelus tabidus* (F.) (Hymenoptera: Tenthredinidae).

Material examined.—**NHM**: 1♂ 'Norbanus scabriculus (Nees), Det. Z. Bouček 1958', 'Rec. in exchange from National Museum Prague, B.M. 1958-342', 'Bohemia or. Velky Vřeštov 25.VI.53 Bouček'; 2♂, 9♀ 'Picroscytus scabriculus Ns., Ch. Ferrière det.', 'Reared from wheat stubble', 'Pres. by Imp. Inst. Ent. B.M. 1935-462', 'Farnham Royal, England, 1935.6.'; 1♂ 'Norbanus scabriculus (Nees), det. Z. Bouček 1975, "no type!"', 'Psilocera verticillata Foerster' (Waterhouse label), 'France', 'cynips aterrima ♂ Schrank'; 2♀ 'Norbanus scabriculus (Nees) ♀, Det. Z. Bouček 1958', 'Rec. in exchange from National Museum Prague, B.M. 1958-342', 'Boh. c.: Praha-Ruzyn, Bouček 25.VII.53'; 1♀ 'Ex. Cephus pygmaeus L.', 'Cambridge 1938', 'D. Berryman'. The following specimens are part of Graham's collection, bearing the same registration label: 'M. W. R. de V. Graham coll., BMNH(E) 1995-489': 1♀ 'France: Vaucluse, Mt. Ventoux, Col de Perrache, 8.VIII.1988'; 1♀, 2♂ same locality, 21.VII.1981; 1♀ same locality, 18.VII.1983; 1♂ same locality, 31.VII.1981; 2♂ same locality, 16.VI.1982; 1♂ same locality, 26.VI.1977; 1♀ '? Fits Nees' des. of scabriculus', 'gena not margined', 'France: Vaucluse nr. Bèdoin, 15.VIII.1981'; 1♀ same locality, 7.VIII.1986; 1♂ same locality, 9.VI.1982; 1♀, 3♂ 'France: Vaucluse, Mt. Ventoux, Massif des Cèdres, 11.VIII.1976'; 1♂ 'France: Vaucluse, Malaucène, Combe de Vaux, 8.VIII.1981'; 2♀, 1♂ 'France: Vaucluse, Roussillon, 9.VIII.1979'; 1♀, 1♂ same locality, 24.VII.1988; 2♂ same

locality, 16.VII.1988; 1♂ 'France: Vaucluse, 1 km S. of St. Gens nr. Beauset, 28.VI.1994'; 1♂ 'France: Vaucluse, nr. St. Didier, 19.VII.1986'; 2♂ 'France: Vaucluse, Malaucène, Crête de St. Armand, 11.VII.1978'; 1♀ 'France: Vaucluse, St. Pierre de Vassols, 23.VII.1977'; 1♀ same locality, 11.VIII.1976; 1♀ 'France: Vaucluse, Dentelles de Montmirail, 4.VIII.1975'; 1♂ 'France: Vaucluse, Grange Neuve, 13.VI.1994'; 1♂ 'France: Vaucluse, St. Didier, 20.8.92'; 1♀ 'France: Drôme, La Poët-en-Percip, 22.VII.1992'; 1♀ same locality, 25.VI.1991; 1♀ 'France: Drôme, Col de Macuègne, 18.VII.1991, Pastinaca'; 1♀ 'meridionalis Masi', same locality, 7.VIII.1975; 1♂ same locality, 13.VIII.1983; 1♂ same locality, 21.VIII.1986; 1♂ same locality, 1.VIII.1979; 1♀, 1♂ 'France: Drôme, Col de l'Homme Mort, 22.VII.1990'; 1♂ same locality, 4.VII.1990; 1♂ same locality, 18.VIII.1990; 1♂ 'France: Alpes de Haute Prov., Redortiers, 12.VII.1988'; 1♂ same locality, 15.VII.1986; 1♀ 'France: B/Rhône, La Crau, near Mas St. Claude, 3.VII.1991'; 1♂ 'France: Gard, Causse de Blandas, 8.VIII.1984'; 1♀ 'Picroscytus ?meridionalis', near syntypes of meridionalis, 17.3.70', 'Slovakia, Šturova, bank of Danube, 22.7.1963'; 1♂ 'Czechoslovakia: Slovakia: Kovačovské Kopce, 7.VI.1958 Hoffer'. **NHMHV**: 1♀ 'Weiden a. Neusiedl. See 12.VII.1914 Ruschka leg.', 'Norbanus scabriculus (Nees) det. Z. Bouček 1956'; 1♀ 'Collect. G. Mayr', 'Pter. Scabriculus N. det. Förster', 'Micr. Praep.', 'Pteromalus scabriculus Nees Or. Es.', 1♀ '7.V.16 Pfaffstätten', 'Umg. Wien leg. Ruschka', 'P. scabriculus N. det. Ruschka 19'; 2♀ 'Tolmein', 'Collect. Graeffe', 'Pteromalus scabriculus N. ♀ det. Ruschka 1919'. **MICO**: 1♀ 'Norbanus scabriculus (Nees) ♀, det. M. Mitroiu 2008', 'RO, CT, R.N. Agigea, 9.VII.00, leg. I. Popescu'; 1♂ 'Norbanus scabriculus (Nees) ♂, det. M. Mitroiu 2008', same locality, 4.VII.2000, leg. I. Popescu; 1♀ 'Norbanus scabriculus (Nees) ♀, det. M. Mitroiu 2008', 'RO, IS, R.N. Valea lui David, 6.VIII.2000, leg. M. Mitroiu'; 2♀ 'Norbanus scabriculus (Nees) ♀, det. M. Mitroiu 2008', same locality, 5.VIII.1999, leg. M. Mitroiu.

***Norbanus (Norbanus) tenuicornis* Bouček**
(Fig. 3)

Norbanus tenuicornis Bouček 1970.

Diagnosis.—The only *Norbanus* species having the postmarginal vein much shorter than the marginal vein (cf. Fig. 3). Basal

cell completely bare. Very minute species (usually less than 2 mm) with long and slender antennae.

Distribution.—Canary Islands, China, Italy (Noyes 2003). Previously not recorded for Spain (mainland).

Biology.—Unknown.

Material examined.—**Type material.** **NHM**: 'Italia: Ortovero nr. Albenga, 5.X.69 Bouček', 'Holotypus ♀ *Norbanus tenuicornis* Bouček 1970', 'Presented to BMNH 1974, Z. Bouček', 'B.M. TYPE HYM 5.2329'. **Additional material.** **NHM**: 6♀ 'N. *tenuicornis* Bčk, ♀, Z. Bouček det. 1975' (1♀ det. 1973), 'Italy, Ceriale nr Albenga, 3.IX.72 Bouček'; 2♀ 'N. *tenuicornis* Bčk, ♀, det. Z. Bouček 1975', 'Villasimius, S. Sardinia, VI.75 Bouček'; 6♀ 'N. *tenuicornis* Bčk. ♀, det. Z. Bouček 1975' (1♀ det. 1973), 'Spain: Castellón, Benicasim, 13–15.VI.73 Bouček'; 1♀ 'N. *tenuicornis* Bčk, ♀, det. Z. Bouček 1975', same locality, 22–24.VI.74 Bouček; 3♀ 'N. *tenuicornis* Bčk. ♀, det. Z. Bouček 1975' (1♀ det. 1974), 'Spain (Murcia): Sra. de Espuña, nr. Totana, 20.VI.1973 Z. Bouček BM 1973-312'; 2♀ 'N. *tenuicornis* Bčk, ♀, det. Z. Bouček 1975', 'Spain: Murcia, nr Manzarrón, 21.VI.1973, Z. Bouček BM 1973-312'; 3♀ 'N. *tenuicornis* Bčk, ♀, det. Z. Bouček 1975' (1♀ det. 1973), 'Spain: Malaga, nr. Nerja, 23.VI.1973 Z. Bouček BM 1973-312'; 1♀ 'N. *tenuicornis* Bčk, ♀, det. Z. Bouček 1975', 'Spain (Malaga): Estepona, 29–30.VI.74 Z. Bouček'; 1♀ 'tenuicornis', 'Spain (Malaga): Estepona, 29–30.VI.74 Z. Bouček', 'BM 1974-321'; 1♀ 'N. *tenuicornis* Bčk., ♀, det. Z. Bouček 1975', 'Spain: Granada, La Herradura, 24.VI.1973, Z. Bouček BM 1973-312'; 1♀ 'tenuicornis', same locality, 2.VII.74 Z. Bouček, BM 1974-321.

Subgenus *Picroscytoides* Masi
***Norbanus (Picroscytoides) calabrus* (Masi)**
(Figs 2, 8, 16)

Picroscytus calabrus Masi 1942.

Norbanus calabrus (Masi 1942), Szelényi (1974).

Picroscytoides albiventris Bouček 1969, Bouček (1990).

Norbanus (Picroscytoides) calabrus (Masi 1942), Dzhanokmen (1999).

Diagnosis.—The female of this rather robust species can be distinguished from all the other species of the subgenus

mainly by its strongly developed quadrangular lamina at the base of the gena (cf. Fig. 16). The male is quite similar to that of *N. (P.) guyoni*, but differs in its longer antennae and gaster coloration.

Distribution.—Azerbaijan, Croatia, Czech Republic, Italy, France, Kazakhstan, Serbia, Slovakia, Tadzhikistan, Turkey, Turkmenistan (Noyes 2003); Bulgaria, Ukraine (Bouček 1969). Unknown for Cyprus before this study.

Biology.—Unknown.

Material examined.—**Type material.** GNHCM: 1♀ 'Holotype', 'Picroscytus (Masioscytus) calabrus n. sp. typus!', 'subg. Masioscytus, secondo Széleányi (1941)', 'Soveria mannelli (Cal. Sila) 20-VI-29 C. Confalonieri', 'Museo Civico di Genova'. **NHM:** 1♀ 'Sandanski, Bulgaria m. Kourek, 28.V.67', 'Paratypus ♀, Picroscytoidea albiventris Bouček'; 1♂ 'Slovakia mer. Kamenica n/Hr. Bouček 23.7.63', 'Paratypus ♂ Picroscytoidea albiventris Bouček'; 1♂ 'Biograd na m. Jugoslavia, Bouček 14.VII.68', 'Paratypus ♂ Picroscytoidea albiventris Bouček'; 1♂ same information, 19.VII.68. **Additional material.** **NHM:** 2♀ 'albiventris Bčk', 'Norbanus calabrus (Masi), det. Z. Bouček 1996', 'M. de V. Graham, France: B. du Rhône, Fonscolombe, 16.VIII.90'; 2♀ 'Picroscytoidea sp.', 'Cyprus: Limassol, 12.V.1934, G.A. Mavromoustakis BM 1935-55', 'British Museum Loan No. 7214'; 1♀ same information, 1.VI.1934; 26♂ 'Picroscytoidea albiventris Bčk, det. Z. Bouček 1975', 'Villasimius, S. Sardinia, VI.75 Bouček'; 6♂ 'Norb. calabrus (Masi), det. Z. Bouček 1986', 'M. de V. Graham, France: B. du Rhône, Fonscolombe, 16.VIII.90'; 1♂ 'Norbanus guyoni Gir ♂', 'Norbanus calabrus (Masi), det. Z. Bouček 1986', 'Mte Vergine, Avellino, 2.IX.54'. The following specimens are part of Graham's collection, bearing the same registration label: 'M. W. R. de V. Graham coll., BMNH(E) 1995-489': 1♀, 1♂ 'France, B du Rhone, Fonscolombe, 14.VIII.1986; 1♀ same locality, 17.VII.1986; 2♀ same locality, 17.VII.1990; 3♀, 15♂ same locality, 16.VIII.1990; 1♂ same locality, 10.VII.1986; 1♂ same locality, 5.VI.1985; 1♂ same locality, 7.VII.1990; 1♂ same locality, 7.VIII.1990; 1♂ same locality, 26.VII.1983; 1♀ 'France: Hérault betw. Soubes and Grandmont, 16.VIII.1975'; 1♀ same locality, 24.VIII.1975; 1♂ 'France: Vaucluse nr. Bédoin,

11.VIII.1986; 1♂ 'France: Vaucluse St. Pierre de Vassols, 6.VIII.1976'; 1♂ 'France: Gard Vic, nr. Blauzac, 22.VII.1977'.

Norbanus (Picroscytoidea) cerasiops (Masi)

(Figs 12, 17)

Picroscytoidea cerasiops Ruschka in Masi 1922 (see the notes on the species author).

Norbanus cerasiops (Masi 1922), Bouček (1990).

Norbanus (Picroscytoidea) cerasiops (Masi 1922), Dzhankomen (1999).

Diagnosis.—The species is close to *N. (P.) obscurus*. Both sexes differ from it in their body coloration; the female also differs in having the antennae ending without a clear spicula and the male in having the antennae (pedicellus plus flagellum) shorter than head width (cf. Fig. 12, 17).

Distribution.—Croatia, Cyprus, Czech Republic, France, Hungary, Italy, Kazakhstan, Republic of Moldavia, Morocco, China, Romania, Serbia, Slovakia, Spain, Turkey (Noyes 2003); previously unrecorded for Greece and Madeira.

Biology.—This species is known to be a primary parasitoid of various Curculionidae (Coleoptera): *Larinus planus* (F.), *L. turbinatus* Gyllenhal, *Lixus brevirostris* Boheman, *L. cardui* Olivier, *L. juncii* Boheman, *L. scabricollis* Boheman (Noyes 2003). Possibly it also acts as a secondary parasitoid through various other parasitic wasps such as *Bracon intercessor* Nees (Braconidae) or *Eurytoma* sp. (Eurytomidae) (Graham 1969). In this study it is recorded for the first time as a parasitoid of *Lixus ascanii* (L.) on *Crambe tatarica* Sebeok.

Notes on the species author.—In his paper of 1922, Masi clearly attributed this species to Dr. F. Ruschka, from whom he received a specimen labelled "*Cerasiops mediterraneus* g. et sp. n.". He recognized this individual as a conspecific of his own *N. cerasiops* specimens and congeneric of *N. obscurus*, described by Masi himself in the same paper (*sub Picroscytoidea obscurus* Masi 1922). Believing "*Cerasiops*" unsuit-

able as a genus name for his *N. obscurus*, he described the new genus *Picroscytoides* and changed the name of Ruschka's species in *P. cerasiops* (Ruschka) (Masi 1922, p.151). The paternity of the species is clearly attributed by Masi to Ruschka also in the description, in which the name *Picroscytoides cerasiops* is followed by "(Ruschka) in litt." (Masi 1922, p. 154). However, since Ruschka did not satisfy the criteria of availability, i.e. he did not publish a description of his new species, the authorship of this species belongs to Masi.

Material examined.—**Type material.** GNHCM: 1♂, 'Syntype', 'Picroscytoides cerasiops Masi, 1922', 'Is. Giglio, VII-1902, G. Doria', 'Museo Civico di Genova'; 3♂ same locality; 1 antenna 'Syntype', 'Antenna di Picroscytoides cerasiops Ms. ♂ Is. Giglio'. **Additional material.** NHM: 1♀ 'Norbanus (P.) cerasiops (Masi), Dzhankmen, 23.VI.80' [in Russian]; 1♀ same data, 17.VI.80; 1♂ same data, 8.VI.80; 4♀ 'Picroscytoides cerasiops Masi, Zd. Bouček det. 1975', 'Villasimius, S. Sardinia, VI.75 Bouček', 'BM 1975-280'; 1♀ 'Picroscytoides cerasiops Rusch. [sic], det. Z. Bouček 1980', 'Greece: Thessalia Nr. Kalambaka Pinios riverbed, 14–20.VII.1979, BM 1979-312, M.C. Day, G.R. Else, D. Morgan'; 1♀ 'Picroscytoides cerasiops Masi, det. Z. Bouček 1974', 'Spain (Malaga): Ronda, 1.VII.1974 Z. Bouček'; 1♀ 'Picroscytoides cerasiops Masi, det. Z. Bouček 1974', 'Spain (Malaga): Estepona, 29–30.VI.74 Z. Bouček'; 1♀ 'cerasiops Masi', 'Picroscytoide', 'Spain (Madrid): El Pardo, 10.VII.1974 Z. Bouček'; 2♀, 4♂ 'Picroscytoides cerasiops Masi, Ch. Ferriere det.', 'Morocco, Rabat, VII.1936, M. Bremond, Ex. larva of Lixus No. 3', 'Pres. by Imp. Inst. Ent., BM 1937-132'; 1♂ 'Cyprus: Limassol, 29.V.1934 G.A. Mavromoustakis, BM 1935-55', 'British Museum Loan No. 7214'; 1♂ 'Picroscytoides', 'Cyprus: Zakaki, 5.VII.1934 G.A. Mavromoustakis, BM 1935-55', 'British Museum Loan No. 7214'; 1♀ 'Picroscytoides cerasiops Masi, Ch. Ferriere det.', 'Cyprus: Limassol, 15.V.1921 G.A. Mavromoustakis', 'Pres. by Imp. Inst. Ent., BM 1929-43', '1♀ 'Mallorca, Magaluf, 3-9.7.1975 K.M. Guichard'; 3♂ 'cerasiops', 'Spain (Granada): La Harradura, 2.VII.74 Z. Bouček', 'BM 1974-321'; 2♂ same locality, 24.VI.1973, 'Z. Bouček, BM 1973-312';

1♂ 'Spain: Toledo, 6.VII.1974, Z. Bouček', 'BM 1974-321'; 1♂ 'Spain: Murcia, Sra. de Espuña nr. Totana, 20.VI.1973', 'Z. Bouček, BM 1973-312'. The following specimens are part of Graham's collection, bearing the same registration label: 'M. W. R. de V. Graham coll., BMNH(E) 1995-489': 2♀ 'cerasiops', 'sp. indet. B', 'France: Vaucluse, Dentelles de Montmirail, 15.VII.1974'; 1♀ 'France: Vaucluse, nr. Bèdoin, 23.VII.1984'; 1♀ same locality, 6.VII.1983; 1♂ same locality, 10.VI.1985; 1♀ 'cerasiops R.', 'France: Hérault betw. Soubes and Grandmont, 16.VIII.1975'; 1♀ 'France: B du Rhone, Fonscolombe, 24.VII.1984'; 1♀ same locality, 17.VII.1990; 1♀ 'Madeira: Curral dos Romeiros, 26.VII.1982'. **MICO:** 1♂ 'Norbanus cerasiops (Masi) ♂ det. M. Mitroiu 2005', 'P.N. Măcin, Culmea Pricopanului, capc. Malaise, 23.07.–25.07.04'; 1♂ 'Norbanus cerasiops (Masi) ♂ det. M. Mitroiu 2008', 'ex. Lixus ascanii (L.) in Crambe tatarica, 9.VII.2002', 'Romania, IS, R.N. Valea lui David, leg. M. Mitroiu'.

Norbanus (Picroscytoides) guyoni (Giraud)

Arthrolysis guyoni Giraud 1869.

Picroscytoides guyoni (Giraud 1869), Bouček (1969).

Norbanus guyoni (Giraud 1869), Bouček (1990).

Diagnosis.—The female can be easily separated from all the other species of the subgenus by its large body size (about 1 cm) and its very long and conical, mainly orange, gaster. The male is similar to that of *N. (P.) calabrus*, but differs in its shorter antennae and gaster coloration.

Redescription.—Even if very careful for that time, Giraud's description lacks many details. Types of *N. (P.) guyoni* are probably lost and Masi (1922) considered the species of uncertain validity. Subsequent authors regarded it as a valid species, but no further diagnostic character has been given since its description. So we provide a redescription of both sexes.

Female.—Head black, with slightly metallic reflections; eyes red; scape, pedicellus and second annellus light brown, scape lighter at base; first annellus yellow; the rest of the funicle dark brown, with the

distal part of every segment slightly lighter. Mesosoma cupreous, with greenish reflections; tegulae and venation light brown; legs entirely light brown, the anterior and posterior coxae with darker bases. Gaster with the anterior 2/3 brown-orange and the posterior 1/3 blackish, the latter with slightly metallic reflections; the lateral sides of each gastral segment with diffuse brownish spots. Body length: 11 mm. Head very slightly wider than the mesosoma, width about $2.4\times$ length in dorsal view and $1.35\times$ height in frontal view; POL about $1.2\times$ as long as OOL; temple about $0.4\times$ as long as eye length in dorsal view; eye height about $1.3\times$ length; malar space about $0.8\times$ as long as eye height; gena strongly carinate; head sculpture very superficial, especially the frons; vertex covered with numerous white hairs; lower margin of toruli slightly above lower eye margin; antennal formula: 11262; combined length of pedicellus and flagellum about as long as head width; scape exceeding the vertex, equal to eye height; pedicellus dorsally about $2.1\times$ as long as wide; the first annellus transverse, the second approximately quadrate; all funicular segments (F) longer than wide, F1 length about $3.6\times$ width, F6 about $1.9\times$; clava about as long as F6 plus $1/2$ of F5, with a gradually narrowing spicula, the suture slightly evident; F1–F2 with 7 rows of sensillae, F3–F4 with 5 rows, F5–F6 with 4 rows, the claval segments with 3 rows. Mesosoma length about $1.3\times$ width; mesoscutum width about $1.6\times$ length; scutellum width about $1.2\times$ length; propodeum width about $6.2\times$ length in median part, uniformly reticulated; spiracles very large and elongate; callus covered with white dense hairs; anterior wings hyaline and triangular, length about 2.6 width; basal cell and basal vein glabrous; speculum very narrow, under the parastigma and the marginal vein; disc covered with short and dense pilosity; marginal vein : post-marginal vein : stigmal vein = 44 : 31 : 20; stigma not large, pointed distally under

uncus. Gaster conical, length about $4.3\times$ width, about twice as long as head plus mesosoma; posterior margin of the first tergite with 3 lobes; the more intense pigmented areas covered with numerous white hairs.

Male.—Differs from female as follows: green reflections on head and mesosoma stronger; all coxae and femora darker, tibiae yellow; gaster orange with its tip black, without lateral dark spots, ovate and much shorter; antennae thin, with long erect setae and no knots; antennal formula: 11272; combined length of pedicellus and scape about $1.2\times$ as long as head width; temple about $0.3\times$ as long as eye length. Body length: 5 mm.

Distribution.—Algeria (Giraud 1869) (see the notes on type locality and distribution). Previously unrecorded for Libya.

Biology.—Primary parasitoid of *Oecocercis guyonella* Guenée (Lepidoptera: Gelechiidae) (Giraud 1869; Herting 1975).

Notes on type locality and Distribution.—*Norbanus guyoni* has been considered until now as a European and North African species, probably due to a misunderstanding regarding the type locality, which, according to some authors, might include France (Noyes 2003). However Giraud never mentioned France in his paper (Giraud 1869). Instead, comparing *N. scabriculus* to *N. guyoni* he refers to his species as “l’espèce algérienne”, and cites *N. scabriculus* as “le seul représentant européen que je connaisse de ces genre” (Giraud 1869, p. 484). He also cites both the host (the Lepidoptera gall maker *Oecocercis guyonella*) and its host plant, *Limoniastrum guyonianum* Dur. ex Boss., stating that he received the galls from Dr. Guyon, member of the Institute of France, who was in Algeria in 1847 (Giraud 1869, p. 476). Today *L. guyonianum* is known as a North-Saharan endemic species. Its describer, Michel Charles Durieu de Maisonneuve, was a French botanist, who in 1840–44 was a member of a committee for scientific exploration of Algeria. Moreover,

apart from *N. guyoni*, Giraud (1869) in his work described four more species emerging from *O. guyonella* galls. The first two were the Braconids *Rhaconotus ollivieri* (Giraud) (= *Hormiopterus ollivieri* Giraud 1869), and *Apanteles gallicolus* (Giraud) (= *Microgaster gallicolus* Giraud 1869), the first of which was named after Dr. Ollivier, an Algerian researcher who collected and sent to Giraud another parcel of galls (Giraud 1869, p. 480). The third was the Torymid *Microdontomerus albipes* (Giraud) (= *Callimome albipes* Giraud 1869), for which Grissell (1995) clarified the Algerian origin, and the fourth was *Eupelmus gueneei* Giraud (1869), which together with *N. guyoni* is still considered also an European species, with France as type locality (Noyes 2003). We think that all these elements make clear that all the parasitoids of *O. guyonella* described by Giraud (1869), including *N. guyoni*, are from Algeria originally.

Material examined.—NHM: 1♂ '*Picroscytoidea guyoni* (Giraud), Z. Bouček det. 1972', 'Biskra, Algeria, galls *Limoniastrum guyonianum* ex. 23.IV.1904, Wism. 1910-166'; 2♂ '*Picroscytoidea guyoni* (Giraud), Z. Bouček det. 1973', 'Cyrenaica: Bersis (W of Tocra) 26.VII.1957', 'K.M. Guichard, BM 1957-669'.

***Norbanus (Picroscytoidea) laevis* Bouček**

Picroscytoidea laevis Bouček 1969.

Norbanus laevis (Bouček 1969), Bouček (1990).

Norbanus (Picroscytoidea) laevis (Bouček 1969), Dzhanokmen (1999).

Diagnosis.—According to Bouček (1969), this species can be easily recognized by its long pilosity and the obliterated sculpture of the head and mesosoma. Although no material was available for our study, Bouček's description clearly differentiates this species from other *Norbanus*.

Distribution.—Azerbaijan, Kazakhstan, Uzbekistan (Bouček 1969; Dzhanokmen 1999).

Biology.—Primary parasitoid of *Myelois cinctipalpella* Christ (Lepidoptera: Pyrali-

dae) on *Carthamus tinctorius* L. (Asteraceae); also associated with *Ferula songorica* Pall. ex. Spreng. (Apiaceae) (Bouček 1969).

***Norbanus (Picroscytoidea) obscurus* (Masi)** (Figs 14, 15, 20, 21)

Picroscytoidea obscurus Masi 1922.

Norbanus obscurus (Masi 1922), Bouček (1990).

Norbanus erdoesi (Szelényi 1974); **syn. n.**

Norbanus (Picroscytoidea) obscurus (Masi 1922), Dzhanokmen (1999).

New synonymy.—Comparing the types of *N. obscurus* (Masi) and *N. erdoesi* (Szelényi) as well as additional specimens of *N. obscurus*, we could not find any constant differences between the two species. Thus we consider *N. erdoesi* to be a junior synonym of *N. obscurus*.

Diagnosis.—This species is close to *N. (P.) cerasiops* and *N. (P.) calabrus*. From the former, both sexes differ in their body coloration; the female also differs in its thinner antennae, with clear spicula (cf. Fig. 20), and the male in having the antennae with pedicellus plus flagellum longer than head width. From the latter, both sexes differ mainly in lacking a strongly developed lamina at the mouth corner (cf. Fig. 15); the male also differs in having wide antennal segments, without whorls of long setae (cf. Fig. 21).

Distribution.—Azerbaijan, ex Czechoslovakia, Croatia, Germany, Hungary, Italy, Kazakhstan, Macedonia, Romania, Serbia, Spain, Turkey, Ukraine (Noyes 2003). Newly recorded from Algeria, France, Hungary, Russia, and Syria.

Biology.—Primary parasitoid of *Cephus pygmaeus* L. (Hymenoptera: Cephidae) in stems of Gramineae (Szelényi 1974). Also associated with stems of *Halogeton* (Amaranthaceae) (Dzhanokmen 1999).

Material examined.—**Type material.** GNHCM: 1♀ 'Paralectotype', '*Picroscytoidea obscurus* Ms. Cotypl! ♀♂', 'Is. Giglio, VII-1902, G. Doria', 'Museo Civico di Genova'; 2♂ '*Picroscytoidea obscurus* Masi PLT det. Z. Bouček, 1990', same locality and data. **HNHM:** 1♀ 'Holotypus

Picroscytoidea erdoesi Szélényi ♀, 'Hym. Typ. No. 4246 Mus. Budapest', 'Hungarian Natural History Museum Hymenoptera Coll. Budapest', '*Picroscytoidea erdoesi* sp. n. Det. Dr. Szélényi', '7988', 'Ex *Cephus pygmaeus*', 'Békásmegyer 16.VIII.1956 leg. Dr. Szélényi'; 1♀ '*Paratypus Picroscytoidea erdoesi* Szél. ♀, 'Hym. Typ. No. 4248 Mus. Budapest', 'Hungarian Natural History Museum Hymenoptera Coll. Budapest', '*Picroscytoidea erdoesi* sp. n. Det. Dr. Szélényi', '8560', 'Ex larva *Cephus pygmaeus*', 'Debrecen 10-30.VII.1957 leg. Koppány'. **Additional material.** **NHM:** 1♀ '*Picroscytoidea obscurus* Masi', 'Turkey: Amasya, 30 km. Amasya-Mecitozu, 1.VIII.1960. 3.000'', 'Guichard and Harvey, BM 1960-364'; 1♂ 'Stood under *Picroscytoidea* sp.', same data; 1♂ '*Norbanus obscurus* Masi det.', same data; 1♀ '*Picroscytoidea obscurus* Masi, det. Z. Bouček 1987', 'Spain, Sevilla Carmona, V.1987, Sp. 172.5 ex', 'Cephidae on wheat, CIE A19167'; 1♀ '*Picroscytoidea obscurus* Masi, det. Z. Bouček 1978', 'Algeria: Tadjerouna, V.1943', 'K.M. Guichard, BM 1945-39'; 1♀ '*Picroscytus scabricula* Nees, Ch. Ferrière det.', '20.VI.1927', 'South Russia, Sent by Rostov-on-Don Agric. Exp. Sta. / Pres. by Imp. Inst. Ent., BM 1928-54'; 6♂ '*Picroscytoidea* ?*obscurus* Masi, det. J.S. Noyes 1989', 'Syria: Tel Hadya, VII-IX.1988, R.H. Miller #5', 'ex *Cephus pygmaeus* on wheat'. The following specimens are part of Graham's collection, bearing the same registration label: 'M. W. R. de V. Graham coll., BMNH(E) 1995-489': 1♀ '*obscurus* (Masi)', 'France: B du Rhone, Fonscolombe, 14.VI.1986'; 1♀ same locality, 2.VI.1987; 1♀ same locality, 4.VIII.1986; 1♀ 'France: Drôme, Col de Macuègne, 1.VIII.1979; 1♀ same locality, 7.VIII.1975; 1♀ 'v. near Fonscol. No. 93', '? *Obscurus* Masi', 'France: Gard S. of Alès, Domessargues, roadside, 27.VII.1974'; 1♀ 'France: Aveyron, Gorges du Trévezet, 10.VIII.1975'; 1♂ 'France: Dordogne, Thomas nr. Allas, 5.VIII.1974'; 1♂ 'France, Vaucluse Roussillon, 9/8/79, M. de V. Graham'. **MICO:** 1♀, 1♂ '*Norbanus obscurus* (Masi), det. M. Mitroiu 2008', 'Romania, CT, R.N. Agigea, 9.VII.2000, leg. I. Popescu'; 1♀ '*Norbanus obscurus* (Masi) ♀, det. M. Mitroiu 2008', 'Romania, IS, R.N. Valea lui David, 13.08.2000, leg. M. Mitroiu'.

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Into the wood and back: morphological adaptations to the wood-boring parasitoid lifestyle in adult aulacid wasps (Hymenoptera: Aulacidae)

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Abstract.—A substantial sample of the parasitoid wasp family Aulacidae was examined for external morphological characters in the adults that might serve to facilitate ovipositing in and emerging from wood. The character evolution of these traits was evaluated by tracing them on a recently published phylogeny, and their functional anatomy is discussed. Various features might serve as ovipositor guides or to help remove debris during emergence from the wood, and/or to protect vulnerable body parts during emergence. It is possible to infer collaboration between different body parts to achieve the successful completion of these crucial life history stages. Variation among the taxa examined indicates that the contribution of the individual body parts to complete these tasks in some instances have changed during the evolution of the Aulacidae.

Aulacidae comprises 221 extant species belonging to two genera (Turrisi et al. 2009): *Aulacus* Jurine, 1807, with 75 species and *Pristaulacus* Kieffer, 1900 (including the former *Panaulix* Benoit, 1984), with 146 species. Both genera are represented in all zoogeographic regions, except Antarctica (Kieffer 1912; Hedicke 1939; Smith 2001, 2005a, 2005b, 2008; He et al. 2002; Jennings et al. 2004a, 2004b, 2004c; Turrisi 2004, 2005, 2006, 2007; Jennings and Austin 2006; Sun and Sheng 2007a, 2007b; Turrisi et al. 2009; Smith and Vilela de Carvalho 2010). Aulacidae have a fairly good fossil record, with 37 described species (Nel et al. 2004; Jennings and Krogmann 2009). The oldest record is from the Lower Cretaceous, but most fossil species are from the Cenozoic, with taxa recorded from the Upper Eocene of the Isle of Wight, Baltic, and Paris basin amber, and the Oligocene of North America (Nel et al. 2004).

Aulacidae are koinobiont endoparasitoids of wood-boring larvae of Hymenoptera and Coleoptera (Gauld and Hanson

1995; Jennings and Austin 2004). Hosts are larval Xiphydriidae (Hymenoptera) and, more frequently, Buprestidae and Cerambycidae (Coleoptera) (Skinner and Thompson 1960; Barriga 1990; Visitpanich 1994; Turrisi 1999, 2007; Smith 2001; Jennings and Austin 2004).

Parasitizing hosts situated deep within a tough, woody substrate requires the adult wasp to overcome certain obstacles. The challenge can be broken down into three crucial stages: 1) locating the host inside the wood; 2) ovipositing through the wood on or near the host; 3) emerging from the wood after completing the larval development. Information on the adaptations of Aulacidae are rare (Skinner and Thompson 1960; Quicke and Fitton 1995), often being part of more comprehensive studies dealing with parasitoid Hymenoptera in general (Quicke 1997; Vilhelmsen 1997a, 2003a).

The main sources for aulacid biology is Skinner and Thompson (1960), who provided detailed footage of the behaviour of

Aulacus striatus Jurine, 1807 parasitizing *Xiphydria camelus* (Linnaeus, 1758), and Deyrup (1984) in a note on *Aulacus burquei* (Provancher, 1882), a parasitoid of *Xiphydria maculata* Say, 1836. The female of *Aulacus striatus* locates the hole bored by its host, inserts the ovipositor and lays an egg in the egg of the host. When the xiphydriid larva hatches, it contains a small larva of *A. striatus*. The parasitoid larva feeds internally, delaying its development until the host larva has fed for almost a year and is close to the wood surface. Before pupating, the host larva tunnels up to the surface but not through the bark, which is left as a seal. When the host larva is about to pupate, the parasitoid rapidly completes its development, causing the death of the host. The mature parasitoid larva then emerges from the remains of the host and spins a cocoon outside the host in which it pupates. The aulacid imago emerges about two weeks later, by gnawing a hole through the bark and the thin cap of debris left by the host (Skinner and Thompson 1960; Deyrup 1984).

Concerning host location in Aulacidae, the only behavioural information was provided by Visitpanich (1994), who observed a female *Pristaulacus* sp. antennating wood containing potential host eggs and probing the eggs with the antennae as well as the ovipositor. There is no anatomical information indicating the presence of a vibration detecting system similar to the one employed for host detection by other wasps parasitizing wood-boring insects, e.g., Orussidae (Vilhelmsen et al. 2001) and Stephanidae (Vilhelmsen et al. 2008). Since at least some aulacids apparently oviposit through the borehole made by its host (see below), they may rely more on olfactory clues than on vibration detection when attempting to locate a host, as demonstrated for the parasitoid wasp family Ibalidae (Spradbery 1970).

In this paper we investigate the external morphology of the adults of Aulacidae,

discussing possible function of different features during oviposition into and emergence from the woody substrate. We discuss the character evolution of the relevant traits in relation to the recently published phylogeny of the family by Turrisi et al. (2009).

MATERIALS AND METHODS

Taxa examined.—We examined a substantial sample of Aulacidae, containing 54 species: 8 *Aulacus* and 46 *Pristaulacus*, representing about one quarter of the described extant species of the family (Smith 2001; Turrisi et al. 2009). In addition, data on the morphology of seven fossil and about 30 more extant species were included in the discussion on the basis of descriptions and/or recent revisions. The depositories of the material examined are listed below, the acronyms are according to Evenhuis and Samuelson (2004).

AEIC	American Entomological Institute, Gainesville, Florida, U.S.A. (through the courtesy of Dr David R. Smith).
BMNH	The Natural History Museum, London, United Kingdom (Dr Stuart J. Hine).
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A. (through the courtesy of Dr David R. Smith).
CAS	California Academy of Sciences, San Francisco, California, U.S.A. (through the courtesy of Dr David R. Smith).
CNCI	Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada (Dr John Huber).
DBAC	Dipartimento di Biologia Animale "Marcello La Greca", Università di Catania, Museo Zoologico, "Turrisi G.F. Collezione", Italy.

DEI	Deutsches Entomologisches Institut, Müncheberg, Germany (Prof. Joachim Oehlke, Dr Andreas Taeger).	MRSN	Museo Regionale di Storia Naturale, Torino, Italy (Guido Pagliano).
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Dr Sandor Csoz).	MZLU	Museum of Zoology, Lund University, Lund, Sweden (Dr Roy Danielsson).
IBLP	Instytut Badawczy Lesnictwa, Warszawa, Poland (Dr Jacek Hilszczański).	NMW	Naturhistorisches Museum, Wien, Austria (Michael Madl).
ITLJ	National Institute for Agro-Environmental Sciences, Insect Systematic Laboratory, Tsukuba (Ibaraki), Japan (Dr Koji Yasuda, Dr Kazuiho Konishi).	OLML	Oberösterreichisches Landesmuseum, Linz, Austria (Dr Fritz Gusenleitner).
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A. (through courtesy of Dr David R. Smith).	SAMC	South African Museum, Cape Town, Republic of South Africa (Ms. Margie A. Cochrane).
MCFS	Museo Civico di Storia Naturale, Ferrara, Italy (Dr Fausto Pesarini).	USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A. (Dr David R. Smith).
MCNC	Museo de Ciencias Naturales, Canaria Islands: Tenerife, Spain (Dr Gloria Ortega).	ZFMK	Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany (Dr Dirk Rohwedder).
MCSN	Museo Civico di Storia Naturale "G. Doria", Genova, Italy (Dr Roberto Poggi).	ZIN	Zoological Institute of the Russian Academy of Science, St. Petersburg, Russia (Dr Sergey Belokobylskij).
MFNB	Museo Friulano di Storia Naturale, Udine, Italy (Dr Carlo Morandini).	ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Dr Frank Koch).
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève, Switzerland (Dr Bernhard Merz).	ZMUC	Zoological Museum, Copenhagen University, Denmark.
MNHN	Muséum National d'Histoire Naturelle, Laboratoire d'Entomologie, Paris, France (Dr Claire Villemant).	ZSMC	Zoologische Staatssammlung, Munich, Germany (Prof. Dr Klaus Schönitzer, Erich Diller, Dr Stefan Schmidt).
MNMS	Museo Nacional de Ciencias Naturales, Madrid, Spain (Dr Carolina Martin).		
MRAC	Musée Royal de l'Afrique Centrale, Tervueren, Belgium (Dr Eliane De Coninck).		
MSNP	Museo Civico di Storia Naturale di Calci, Pisa, Italy (Dr Pier Luigi Scaramozzino).		

Extant taxa directly examined.—*Aulacus bituberculatus* Cameron, 1899; *A. burquei* (Provancher, 1882); *A. digitalis* Townes, 1950; *A. impolitus* Smith, 1991; *A. pallipes* Cresson, 1879; *A. japonicus* Konishi, 1990; *A. schoenitzeri* Turrisi, 2005; *A. striatus* Jurine, 1807; *Pristaulacus africanus* (Brues, 1924); *P. barbeyi* (Ferrière, 1933); *P. bicornutus* (Schletterer, 1890); *P. boninensis* Konishi, 1989; *P. capitalis* (Schletterer, 1890); *P. chlapowskii* Kieffer, 1900; *P. compressus* (Spinola, 1808); *P. comptipennis* Enderlein, 1912; *P. editus* (Cresson, 1880); *P. edoardo*

Turrisi, 2007; *P. fasciatus* (Say, 1829); *P. fasciatipennis* Cameron, 1906; *P. flavicrurus* (Bradley, 1901); *P. foxleei* (Townes, 1950); *P. galitae* (Gribodo, 1879); *P. gibbator* (Thunberg, 1822); *P. gloriator* (Fabricius, 1804); *P. haemorrhoidalis* (Westwood, 1851); *P. insularis* Konishi, 1990; *P. intermedius* Uchida, 1932; *P. irenae* (Madl, 1990; formerly in *Panaulix*); *P. iridipennis* (Cameron, 1900); *P. kostylevi* (Alekseyev, 1986); *P. krombeini* Smith, 1997; *P. lindae* Turrisi, 2000; *P. longicornis* Kieffer, 1911; *P. minor* (Cresson, 1880); *P. montanus* (Cresson, 1879); *P. morawitzi* (Semenow, 1892); *P. mourguesi* Maneval, 1935; *P. niger* (Shuckard, 1841); *P. occidentalis* (Cresson, 1879); *P. paglianoi* Turrisi, 2007; *P. patrati* (Audinet-Serville, 1833); *P. pilatoi* Turrisi, 2006; *P. resutorivorus* (Westwood, 1851); *P. rex* (Benoit, 1984; formerly in *Panaulix*); *P. rufipilosus* Uchida, 1932; *P. rufitarsis* (Cresson, 1864); *P. ryukyuensis* Konishi, 1990; *P. sexdentatus* Kieffer, 1904; *P. signatus* (Shuckard, 1841); *P. smithi* Turrisi, 2006; *P. stigmaterus* (Cresson, 1864) and *P. strangaliae* Rohwer, 1917, *P. thoracicus* (Westwood, 1841).

Fossil taxa evaluated from descriptions.—*Aulacus eocenicus* Nel, Waller, Ploëg, 2004 from the Lower Eocene of the Paris basin amber (Nel et al. 2004); *Pristaulacus bradleyi* (Brues, 1910), *P. rohweri* (Brues, 1910), and *P. secundus* (Cockerell, 1916) from the Oligocene of Florissant (Colorado, U.S.A.) (Brues 1910; Cockerell 1916); *P. praevolans* (Brues, 1923) and *P. mandibularis* Brues, 1932 from the Upper Eocene of the Baltic Amber (Brues 1923, 1932); *P. velteni* Jennings and Krogmann, 2009 from the Eocene of the Baltic Amber (Jennings and Krogmann 2009).

Methods of examination.—Observation of external features was carried out on dry preserved specimens with stereomicroscopy and SEM. Digital photographs were made using a Nikon Coolpix 4300 4.0 megapixel digital camera and enhanced using Adobe Photoshop CS® software. SEM micrographs were made using a Philips XL-20. Some pinned and air-dried

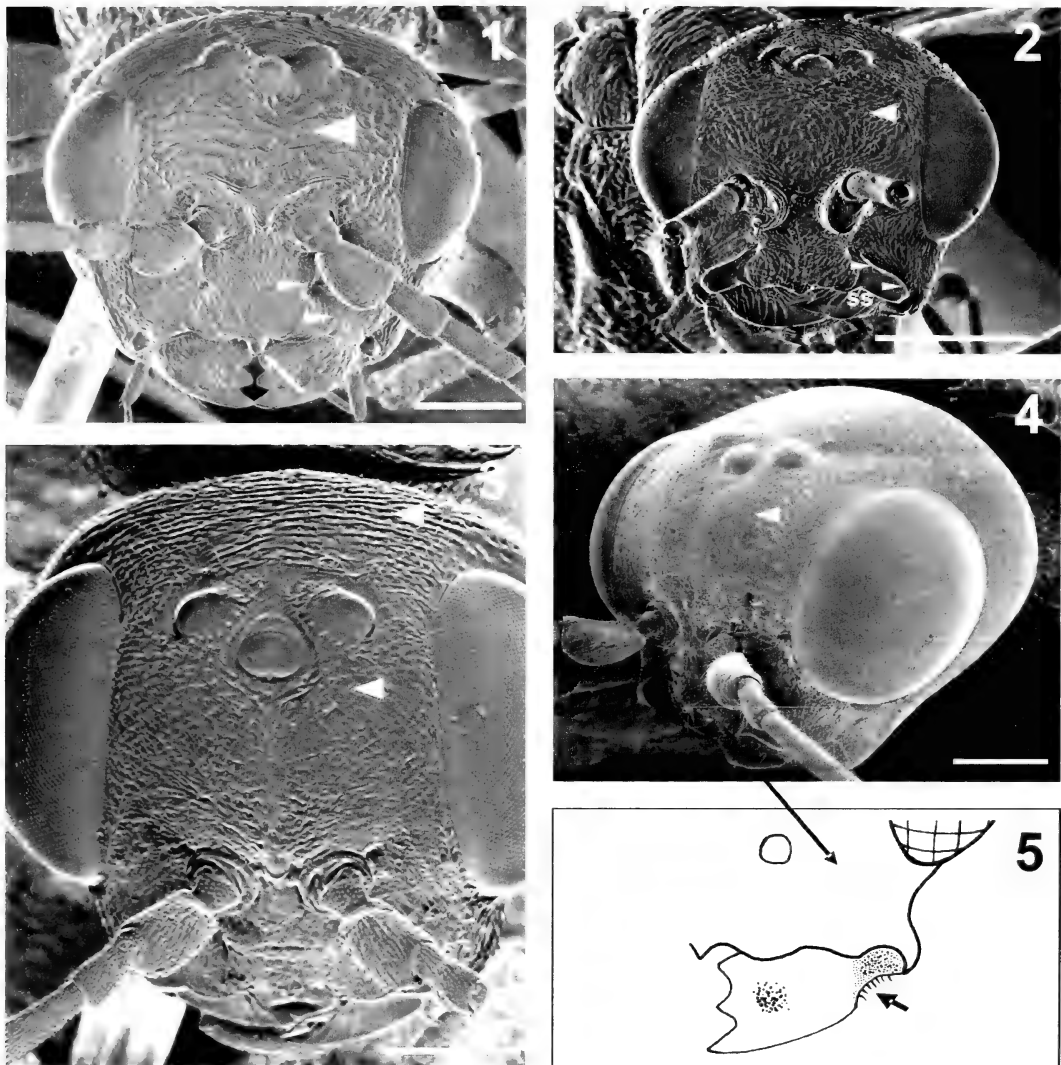
specimens were fixed with Leit-C-plast on an object table and observed at 1.6 kV using a special low voltage anode (spot size: 4–5); other specimens were coated with a Polaron SEM sputter coater system prior to observation at 10 kV using a conventional high voltage anode (spot size: 3–4).

Morphological terms.—Morphological terminology follows Crosskey (1951), Huber and Sharkey (1993) and Gauld and Bolton (1996). Terminology for surface sculpture follows Harris (1979).

RESULTS AND DISCUSSION

Morphological traits of adult aulacids directly observed or taken from literature are reviewed and briefly described in the following and illustrated prior discussing their possible functional value in relation to: 1) oviposition and 2) emergence from the wood.

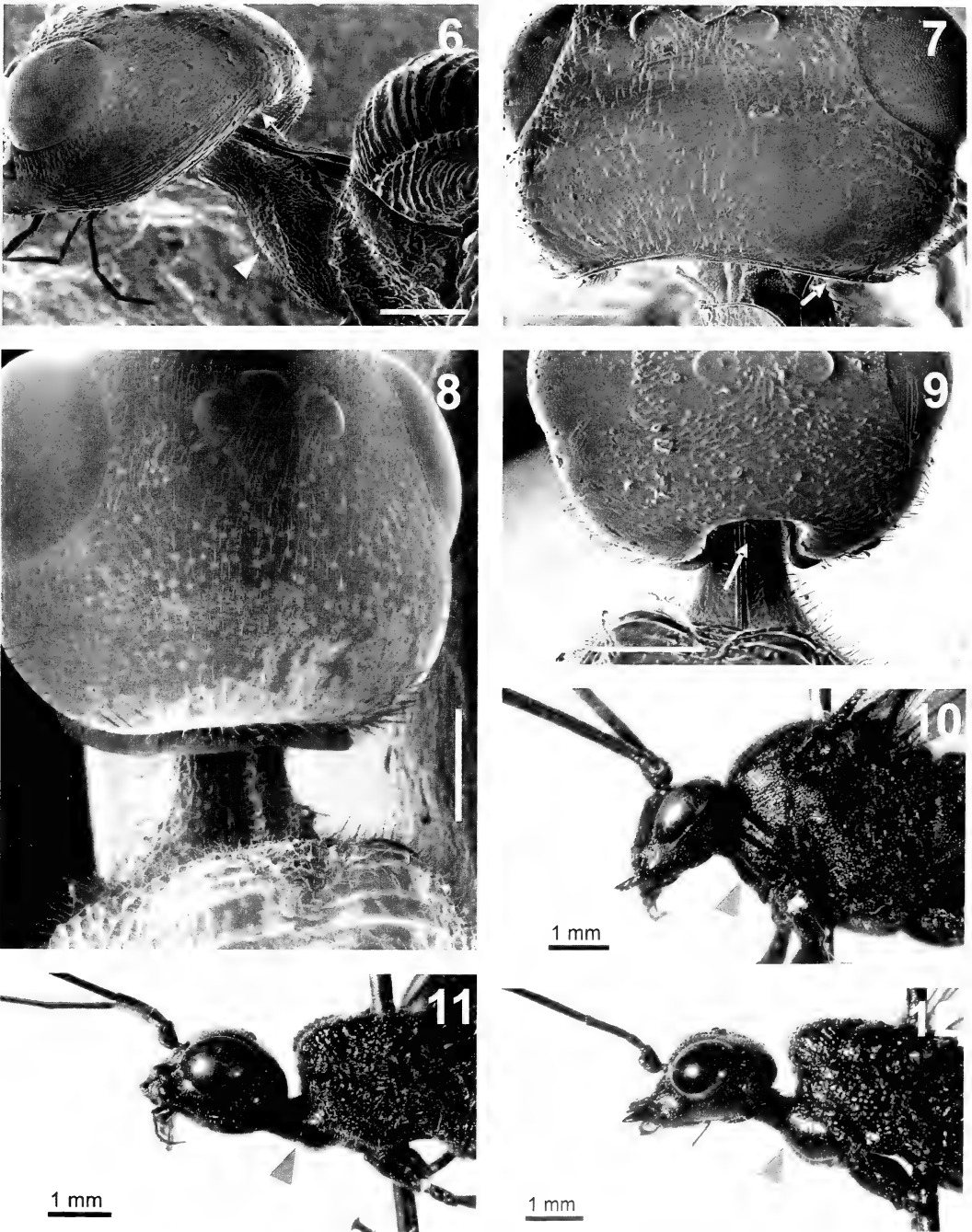
Head.—*Frons and vertex:* The frons is smooth or strongly transverse-carinulate in both fossil and extant *Aulacus* (Fig. 1). A few species of both fossil and extant *Pristaulacus* have the frons weakly transverse-rugulose or striolate-carinulate (Figs 2–3), while most species of this genus, including the fossil *P. velteni* have the frons smooth, at most punctate (Fig. 4). In *Aulacus bituberculatus* and *Pristaulacus tuberculiceps*, the vertex has two prominent posterodorsally directed outgrowths. **Subantennal grooves:** The subantennal grooves are concavities located below the toruli, accommodating the scapes when the antennae are held in a ventral position, e.g., during emergence from the pupa (Vilhelmsen 1997a). The grooves surround the tentorial pits and extend lateroventrally to the lateral areas of the clypeus. The configuration of the subantennal grooves is not known for any fossil species. They are present but not deep in all examined species of *Aulacus* (Fig. 1) and more prominent in all examined species of *Pristaulacus* (Fig. 2). **Clypeus:** All extant species of Aulacidae have a medial process on the



Figs. 1–5. Head of Aulacidae, frontal view: 1, *Aulacus striatus*; 2, *Pristaulacus gibbator*; 3, *Pristaulacus barbeyi*; 4–5, *Pristaulacus compressus*. Larger triangles indicate the sculpture of the frontal area and of the vertex, with or without transverse roughness. Smaller triangles indicate the subantennal groove. Arrow in Fig. 1 indicates the median tooth-like clypeal process. Arrow in Fig. 5 indicates the mandibular groove. Scale bars = 500 μ m.

anterior margin of clypeus, as does the extinct species *Pristaulacus mandibularis*. It is a forward protruding tooth-like process in *Aulacus* and most *Pristaulacus* (Fig. 1), while in *P. rex* it is a lamelliform process. The medial process is indistinct in the fossil *Pristaulacus velteni* (Jennings and Krogmann 2009). **Mandibles:** Both fossil and extant Aulacidae have robust mandibles, with a well developed cutting edge. Moreover, all examined species have a subbasal

transverse groove (Fig. 5) on each mandible. **Posterior margin of the head and occipital carina:** The posterior margin of the head, in dorsal view, is straight or weakly concave in all fossil and nearly all extant species (Figs 6–8). Fossil and extant species of *Aulacus* usually have no occipital carina, except for a few Australasian species where a narrow carina is present (Turrisi et al. 2009). *Aulacus* spp. may have weakly developed transverse-striolate or



Figs. 6–12. Head and anterior part of mesosoma of Aulacidae: 6, *Aulacus striatus* (lateroposterior view); 7, *Pristaulacus gibbator* (dorsal view); 8, *Pristaulacus compressus* (dorsal view); 9, *Pristaulacus comptipennis* (dorsal view). Figs 10–12. Position of the head in relation to the propleura length and to the hind margin of head, lateral view; 10, Unidentified Ichneumonidae; 11, *Pristaulacus comptipennis*; 12, *Pristaulacus compressus*. Arrows indicate the occipital area, without (Fig. 6) or with (Figs 7–8) occipital carina, or with median groove (9). Triangle in Figs 6, 8, 10–12 indicates the propleura. Scale bars = 500 μ m (Figs 6–9).

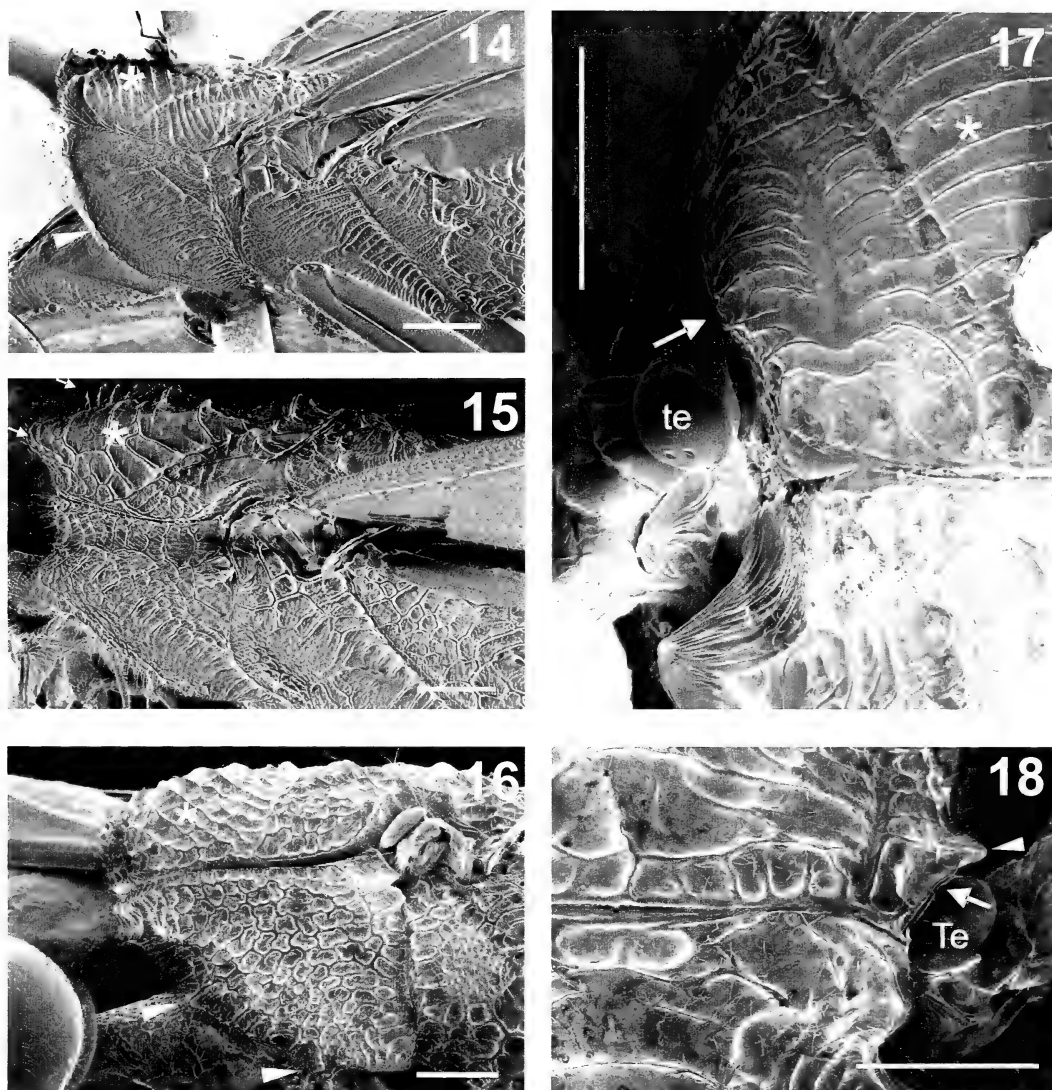


Fig. 13. Lateral view of mesosoma of *Aulacus striatus*. Arrow indicates the anterior margin of mesoscutum. Triangle indicates the lateroventral margin of pronotum. Star indicates the sculpture of mesoscutum. Scale bar = 500 μ m.

rugulose sculpture (Fig. 6) on the occiput. Almost all *Pristaulacus* spp. have an occipital carina, but the occiput is smooth (Figs 7–9). In fossil *Pristaulacus* spp. the carina is very narrow; in extant species it varies from very narrow (Fig. 7) to very wide and lamelliform (Fig. 8), with a width varying from 0.2 to 1.5 \times the diameter of an ocellus. A small clade of extant *Pristaulacus* from the Oriental and Eastern Palaearctic regions, comprising *P. comptipennis*, *P. boninensis*, *P. emarginaticeps*, *P. excisus* and *P. insularis*, is characterized by a more or less wide and deep median groove interrupting the occipital carina medially (Fig. 9).

Mesosoma.—Lateroventral margin of pronotum: The lateroventral margin of the pronotum is rounded and without a tooth-like processes in all *Aulacus* spp., as well as in all fossil and a few extant *Pristaulacus* spp. (Figs 13–14). In the remaining species of *Pristaulacus*, it is angulated anteriorly and more or less acute; moreover, in most species, the lateroventral margin of the pronotum bears one or two anterolaterally directed tooth-like processes (Figs 15–16). **Propleura:** The propleura are elongate in all Aulacidae, forming an extended ‘neck’ between the head and the rest of the mesosoma (Figs 6, 8–9, 11–12). The propleura are less elongate

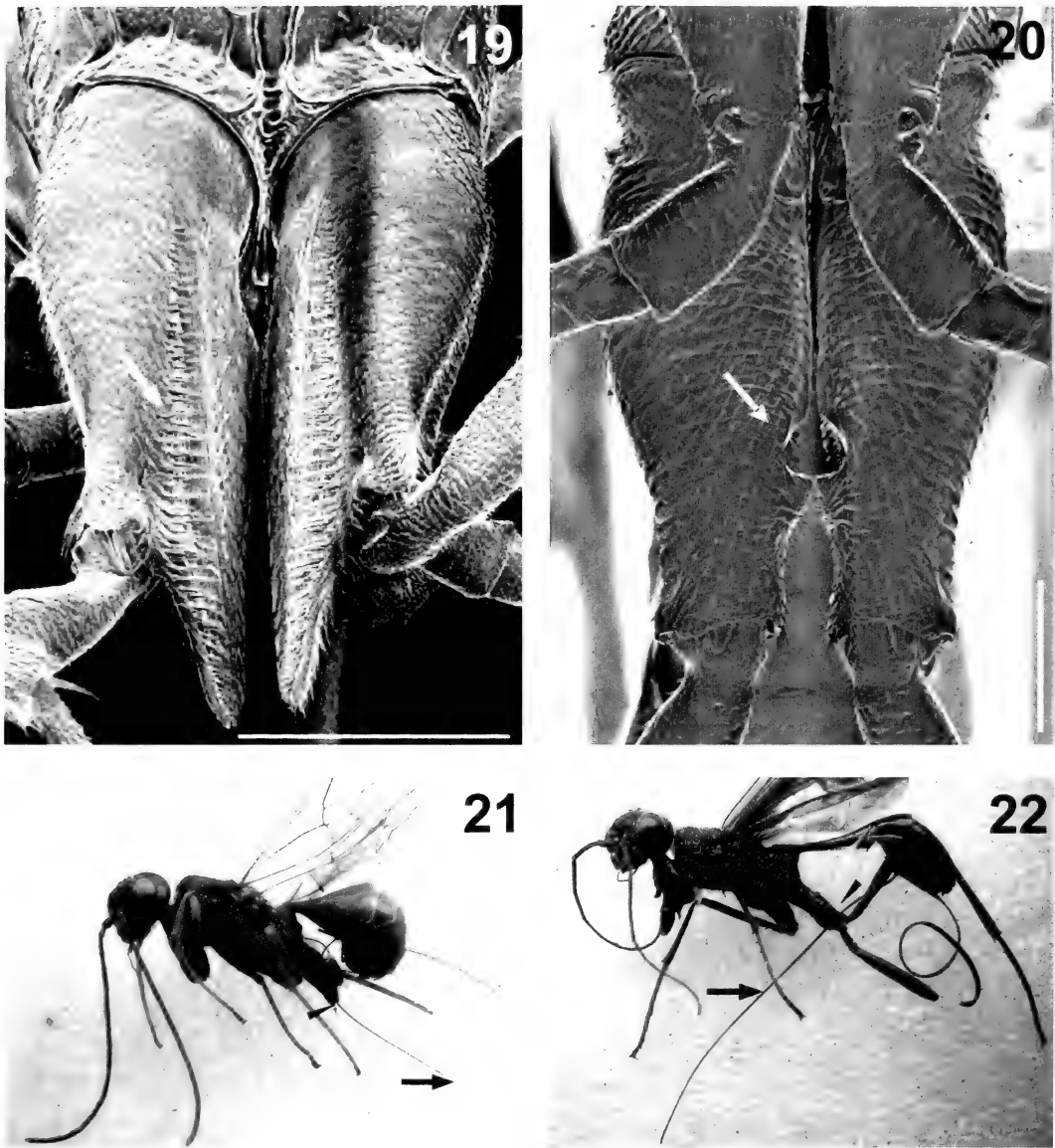
in fossil species. **Sculpture of mesoscutum:** The mesoscutum is weakly sculptured (transverse-carinate) in fossil and extant species of *Aulacus* (Figs 13, 17) and in many fossil species of *Pristaulacus*. However, other fossil species of *Pristaulacus* (e.g., *P. praevolans* and *P. secundus*) have a moderately transverse-carinate sculpture (Cockerell 1916; Brues 1923). In the extant species of *Pristaulacus*, the sculpture varies from weakly (in a few species from Nearctic and Palaearctic Regions) to strongly (in most species) transverse-carinate (Figs 15–17). **Anterior margin of mesoscutum:** In all known fossil taxa, all extant *Aulacus* spp., and most extant *Pristaulacus* spp. the anterior margin of the mesoscutum is rounded in lateral view (Figs 6, 11–13, 16). In some extant *Pristaulacus* spp. it is acute to strongly acute and protruding anteriorly, and in a few species also dorsally (Figs 14–15). **Parascutal carina:** The parascutal carina extends from the anterior part of the mesoscutum to the tegula in all Aulacidae examined. In many fossil and extant taxa the morphology of the mesoscutum is not described in detail. On the basis of a drawing from Cockerell (1916: 103, fig. 9b), the posterior part of the parascutal carina is expanded into a parascutal lobe to cover the tegula in the fossil *Pristaulacus secundus*. In the fossil *Pristaulacus velteni* the parascutal carina is expanded, with tooth-like lateral projection (Jennings and Krogmann 2009). The lobe is absent in the examined extant species of *Aulacus* and no tooth-like process is present above the tegula (Figs 17). In the examined extant species of *Pristaulacus*, the parascutal lobe is present, and most of them have a suprategular tooth-like process (Fig. 18). **Hind coxae:** The configuration of the hind coxae is not known in detail in most fossil taxa. In *Aulacus eocenicus* and a few extant *Aulacus* spp., no groove is present on the medial surface of the coxae. In all other extant species of *Aulacus* a longitudinal (Fig. 19) or (in a few Neotropical species) a transverse hind coxal groove is present.



Figs. 14–18. Mesosoma of Aulacidae: 14, *Pristaulacus kostylevi* (lateral view); 15, *Pristaulacus ryukyuensis* (laterodorsal view); 16, *Pristaulacus compressus* (lateral view); 17, *Aulacus striatus* (dorsal view); 18, *Pristaulacus compressus* (dorsal view). Arrows in Figs 14–16 indicate the anterior margin of mesoscutum. Triangles indicate the lateroventral margin of pronotum; in Fig. 14 there is no tooth-like process; in Fig. 16 two tooth-like processes are present. Arrow in Figs 17–18 indicates the posterior part of the parascutal carina; in Fig. 17 it is without a parascutal lobe and tooth-like supratergular process; in Fig. 18 the parascutal lobe and tooth-like supratergular process (triangle) are present. Star indicates the sculpture of mesoscutum. Te, tegula. Scale bars = 500 μ m.

When a longitudinal groove is present (e.g., *A. striatus*), the hind coxa also has a distal lobe (Fig. 19). A transverse hind coxal groove is present in all extant *Pristaulacus* spp. being situated either subapically (Fig. 20) or, very rarely, subbasally (Turrissi 2006, fig. 15) and the apical lobe is

absent. In the fossil *Pristaulacus velteni* the subapical transverse hind coxal groove is indistinct (Jennings and Krogmann 2009). **Tarsal claws:** (see Turrissi et al. 2009, fig. 11) In all *Aulacus* spp. the tarsal claws have only a very small basal tooth-like process; three tooth-like processes are present in the



Figs. 19–22. Hind coxae (ventral view), hind coxal ovipositor guide, and orientation of ovipositor during oviposition; Figs 19 and 21, *Aulacus* sp.; Figs 20 and 22, *Pristaulacus* sp. White arrow indicates the hind coxal ovipositor guide. Black arrow indicates the ovipositor. Triangle indicates the distal part of hind coxae. Scale bars = 500 μ m (Fig. 19 from Jennings 2006 in *litteris*).

fossil *Pristaulacus praevolans* and *P. velteni* (Jennings and Krogmann 2009); two to six tooth-like processes (mostly four), including the basal one, in the extant species of *Pristaulacus*.

Metasoma.—Petiole: In Aulacidae, the petiole is inserted dorsally on the mesosoma away from the metacoxal foramina,

and it is always fused with the second segment of the metasoma, forming a rigid structure. The petiole is stocky (about as long as wide) in all fossil and most extant species of *Aulacus* (Fig. 21), as well as most fossil and a few extant species of *Pristaulacus*. In most extant *Pristaulacus* spp., the petiole is elongate and slender, between

two and five times longer than wide (Fig. 22). **Ovipositor:** In the fossil *Aulacus eocenicus*, the ovipositor is moderately long, about $0.9\times$ the fore wing length. In other fossil Aulacidae, the ovipositor is not preserved in its entirety. The length of ovipositor is highly variable within extant species. In *Aulacus* spp. it varies from 0.4 to $0.9\times$ of the fore wing length. In *Pristaulacus* spp. it varies from 0.6 to more than $2.0\times$ the fore wing length (usually more than $1.0\times$).

Adaptations for oviposition in wood.—Concerning oviposition, the main problem for hymenopteran parasitoids of xylophagous larvae is to reach the host concealed inside the wood. The tapering and elongate petiole possessed by most extant species of *Pristaulacus* (Fig. 22) together with the dorsal articulation of the petiole possibly allows a wider range of vertical movement of the metasoma with respect to the mesosoma and may improve the handling of the ovipositor. The dorsal insertion of the metasoma facilitates positioning the ovipositor vertically, thus making it possible to employ a long ovipositor (see Vilhelmsen et al. 2001). It has been suggested that the acquisition of the wasp-waist in Apocrita, through the modification of the first metasomal segment, served as a key adaptation to parasitism on hosts living inside wood (Quicke 1997; Vilhelmsen 1997b, 2000). Aulacidae and many other parasitoid wasps with long external ovipositors have transversely subdivided ovipositor sheaths which might facilitate supporting the ovipositor tip in the early stages of drilling (Vilhelmsen 2003a), although aulacids hold their ovipositor sheaths up, away from the substrate.

The cuticle of the ovipositor of Aulacidae is not impregnated with metals, in contrast to some other Hymenoptera that parasitize xylophagous insect larvae (Quicke et al. 1998). This is probably because aulacids oviposit using pre-existing crevices, e.g., the borehole made by the host female during oviposition (Skinner and Thompson 1960), thus obviating the need to

reinforce the ovipositor cuticle for drilling. Instead, the aulacid female employs an ovipositor steering device formed by blocking features at the distal ends of the ovipositor valve interlocking system (Quicke and Fitton 1995). This allows the aulacid to bend the ovipositor tip laterally, thus facilitating guiding the ovipositor through the wood. An additional ovipositor guide in Aulacidae is formed by the hind coxae (Yasumatsu 1937; Jennings and Austin 2004; Turrisi 2004). It is not known whether the species of *Aulacus* without a coxal groove use the hind coxae to guide the ovipositor. In *Aulacus* spp. with a longitudinal hind coxal groove, the coxae when aligned create a longitudinal channel in which the ovipositor is inserted (Fig. 19), guiding it backwards and slightly ventrally (Fig. 21). In all species that have a transverse hind coxal groove, the coxae (Fig. 20), when aligned form a transverse channel guiding the ovipositor anteroventrally (Fig. 22) at an angle depending on the relative positions of the coxae and the metasoma. The internal diameter of this channel is a little wider than the ovipositor, allowing for small movements of the latter and the opportunity for fine steering.

According to Turrisi et al. (2009) the transverse hind coxal groove was acquired very early in the evolution of Aulacidae, even if it is not a ground plan character for the family, and it is retained by most aulacids. A longitudinal hind coxal groove was acquired twice independently within *Aulacus* in a Holarctic clade and by two Australasian species (Turrisi et al. 2009). The shift in orientation of the hind coxal grooves from transverse to longitudinal implies a change in ovipositor mechanism. There seems to be no clear correlation of groove orientation with any of the other features observed (e.g., ovipositor length), and it is at present unclear to us what advantages this reorientation of the ovipositor direction may confer.

The two basalmost extant species of *Aulacus* (*A. wau* and *Aulacus* 'sp. 1') as well

as some fossil taxa (Nel et al. 2004) do not have a hind coxal guide, apparently the plesiomorphic condition within the family. However, Townes (1950) suggested that the absence of the hind coxal grooves may be secondary; this seems to be the case for the small clade *Aulacus brevicaudis* + *A. impolitus* (Turrisi et al. 2009). According to Townes (1950), the absence of the coxal groove was caused by shortening of the ovipositor obviating the need for a structure to guide it. Indeed, both *Aulacus brevicaudis* and *A. impolitus* have comparatively short ovipositors. However, in the fossil *Aulacus eocenicus*, the ovipositor is moderately long, about $0.9\times$ fore wing length, although no hind coxal ovipositor guide is present (Nel et al. 2004).

Adaptations for emerging from wood.—Many structures of parasitoid wasps pupating within wood are possibly emergence-facilitating adaptations, for example to break down and remove the debris plug sealing the pupal chamber, while other structures assure protection of delicate structures such as antennae and wings. To remove the debris plug, aulacids use mainly their mandibles (Skinner and Thompson 1960; Quicke et al. 1998), but the head capsule and mesosoma also participate. The role of the head in making progress through the gallery within the wood is evident from Skinner and Thompson (1960). The wasp moves the head up and down, and also laterally, to cut and remove the debris. The median clypeal process (Figs 1–5) may facilitate crumbling of the plug and penetration of the head into the massive plug. A structure with a similar function is present in other parasitoid wasps (e.g., Stephanidae and some Ichneumonidae) pupating within wood (Quicke 1997).

The outgrowths from the vertex in *Aulacus bituberculatus* and *Pristaulacus tuberculiceps* (clearly an evolutionary convergence) perhaps have a similar function to the ocellar corona (a circlet of cuticular projections around the median ocellus)

observed in Orussidae (Vilhelmsen 2003b) and Stephanidae (van Achterberg 2002), although in the latter two families the projections are in a slightly more anterior position. The ocellar corona has been suggested to be used to brace the head of the wasp while chewing an escape tunnel or help the wasp drag itself along its gallery (Engel and Grimaldi 2004).

A well developed transverse striolate-carinulate sculpture is present on the frons of fossil taxa of both *Aulacus* and *Pristaulacus*, and it is present in several extant species of *Aulacus* (Fig. 1). It is reasonable to assume that this sculpture plays an important role during emergence of the imago of these taxa, since the massive debris plug needs to be reached and cut by the mandibles, and then pushed away (Skinner and Thompson 1960). In other extant *Aulacus* spp. and in most extant *Pristaulacus* spp., the sculpture of the frons is weak or even absent (Figs 2–4), but a more or less developed transverse-carinate sculpture is always present on the mesosoma. Based upon inference from the phylogeny of Turrisi et al. (2009), the sculpture on head and mesosoma arose simultaneously within Aulacidae, suggesting a close functional linkage of these tagmata to help adult emergence from the wood early in the evolutionary history of the family. This is the case of most extant "*Aulacus*" spp. and many fossil aulacids, in which the important role of the head during emergence from wood might have been further facilitated by the presence of an angulated anterior head margin. In contrast, head sculpture is secondarily reduced or lost and the anterior margin of the head is rounded in most extant *Pristaulacus* spp. as well as in a few lineages of extant "*Aulacus*" spp., whereas the mesosomal sculpture remained and still could assume an important role in removal of debris within the wood gallery.

It seems that in the more ancestral species of Aulacidae (i.e., the "*Aulacus*" grade) the head plus the mesosoma share

the tasks of crumbling and removing the debris plug, whereas in more derived aulacids (extant *Pristaulacus* spp.) the head has mainly the task of penetrating, crumbling and cutting the debris. The function of removing the debris is mainly undertaken by the mesosoma. In addition, the mesosoma might serve to brace the body during emergence, leaving the head free to break down the frass plug; the absence of distinct sculpture on the head might make it less prone to get stuck when executing this task. The acute shape of the anterior margin of mesoscutum and the marginal horn-like processes on the pronotum in many extant species of *Pristaulacus* may be interpreted as adaptations to these functions, and thus facilitating the emergence of the imago from the wood gallery (Figs 14–16).

The 'neck' formed by the elongate propleura, a feature shared by all extant Aulacidae (Figs 11–12) as well as the Gasteruptiidae (Turrisi et al. 2009), might also help removing debris. Elongate propleura allow wider movements of the head in the vertical plane and makes it possible to employ the mandibles forward in a prognathous position (Fig. 12; see also below). The occipital carina in *Pristaulacus* spp. possibly serves to protect the occipital area, especially around the foramen magnum, from incursion of debris. The enlargement of the occipital carina, forming an extended lamina dorsal to the neck (Fig. 8) in most extant *Pristaulacus*, would enhance this function. The development of this protective structure is probably correlated with the length of the propleura that increases the distance between head and mesosoma, and exposes the occipital area to penetration by debris. In addition, the enlarged occipital carina might help displacing debris during emergence. The presence of a broad occipital carina might restrict the dorsal tilting of the head due to interference with the propleura (Figs 8, 12). A medial groove is situated on the hind margin of the head in a subclade of

Pristaulacus. The width of the groove is evidently correlated with the width of the propleura (Fig. 9), fitting around them; this enables wider dorsal movement of the head and consequently the mandibles can be employed in a prognathous position (Fig. 11), even more so than in taxa without the medial groove (Fig. 12). The groove allows the wasp to lock its head against the propleura: this might facilitate gaining purchase for the mandibles and pushing away debris with the head.

In some endoxylic parasitoid wasps (e.g., Ibalidae, Stephanidae), cuticular horn-like processes of the body, mainly on the mesosoma, are believed to be adaptations to emerging from hard substrates and for protecting delicate parts of the body (Quicke 1997; Vilhelmsen 1997a). Likewise, it is possible that the presence of one or two tooth-like processes on the lateroventral margin of pronotum in many species of *Pristaulacus* may help pushing the imago along when it ecloses from the wood.

The legs obviously play an important role when the adult wasp moves through the galleries in the wood and emerges from it. According to Turrisi et al. (2009), the presence of a simple claw is a plesiomorphic feature of Aulacidae, and the pectinate claw is an autapomorphy of *Pristaulacus*. In conjunction with this, the increased number of tooth-like processes on the tarsal claws (Turrisi et al. 2009), may be interpreted as another emergence-facilitating adaptation, enhancing the insect hooking against the walls of the tunnel when it pushes forward. Given that the claws are in constant contact with the substrate also after emergence, they might have other functions as well.

During emergence, the antennae and wings of the adult wasp are highly susceptible to damage. The extant species of *Aulacus* have weakly developed subantennal grooves (Fig. 1), while in many extant *Pristaulacus* spp., they are more developed (Fig. 2). The presence of subantennal and mandibular grooves, and the

tendency of the former to become deeper in more derived species (*Pristaulacus* spp.) may be interpreted as adaptations to protect the antennae. During emergence the subantennal and mandibular grooves accommodate the bases of the antenna, whose remaining part is curved poster-oventrally (see also Vilhelmsen 1997a), thus reducing the risk of damage.

The point of articulation of the fore wing is also vulnerable during emergence from the wood. In taxa where a parascutal lobe and sometimes a supratergular tooth-like process are present (e.g., *Pristaulacus* spp.), they probably serve to protect the wing base (Fig. 18) from abrasion against the gallery sides, as opposed to *Aulacus* spp. where these features are absent (Fig. 17).

CONCLUDING REMARKS

In this paper we have argued that many morphological features of the aulacid imago may be interpreted as adaptations to the lifestyle as parasitoid of wood-boring insects. In particular, they might facilitate oviposition into the wood and emergence out of it. The species of *Pristaulacus* appear to be more specialized due to the presence of several morphological features (occipital carina, parascutal lobes and supratergular spines, pectinate tarsal claws) not shared by *Aulacus* spp.

Some adaptations occur in other families of Hymenoptera with a similar life style, including the hind coxal ovipositor guide (Turrisi et al. 2009), found in some Braconidae (Cenocoeliinae) and Ichneumonidae (Labeninae) (Townes 1950; Turrisi 2004), obviously instances of convergence, and the ovipositor steering mechanism (Quicke and Fitton 1995).

In Aulacidae, it is possible to infer cooperation between structures on different body parts (e.g., the median process on the clypeus, the head and mesosoma sculpture, and perhaps the pectinate tarsal claws) during emergence from the wood. Furthermore, the character combinations displayed by different taxa indicate shifts in emphasis of the function of different

body parts (e.g., both head and mesosomal sculpture in *Aulacus* spp. to predominantly mesosomal sculpture in *Pristaulacus* spp. during emergence).

In the present paper we have aimed to show that it is possible to correlate detailed morphology with the intricacies of lifestyle in parasitoid Hymenoptera. We hope that it will inspire further studies that will elucidate this diverse and biologically important life style, both within Aulacidae and in other parasitoid wasps.

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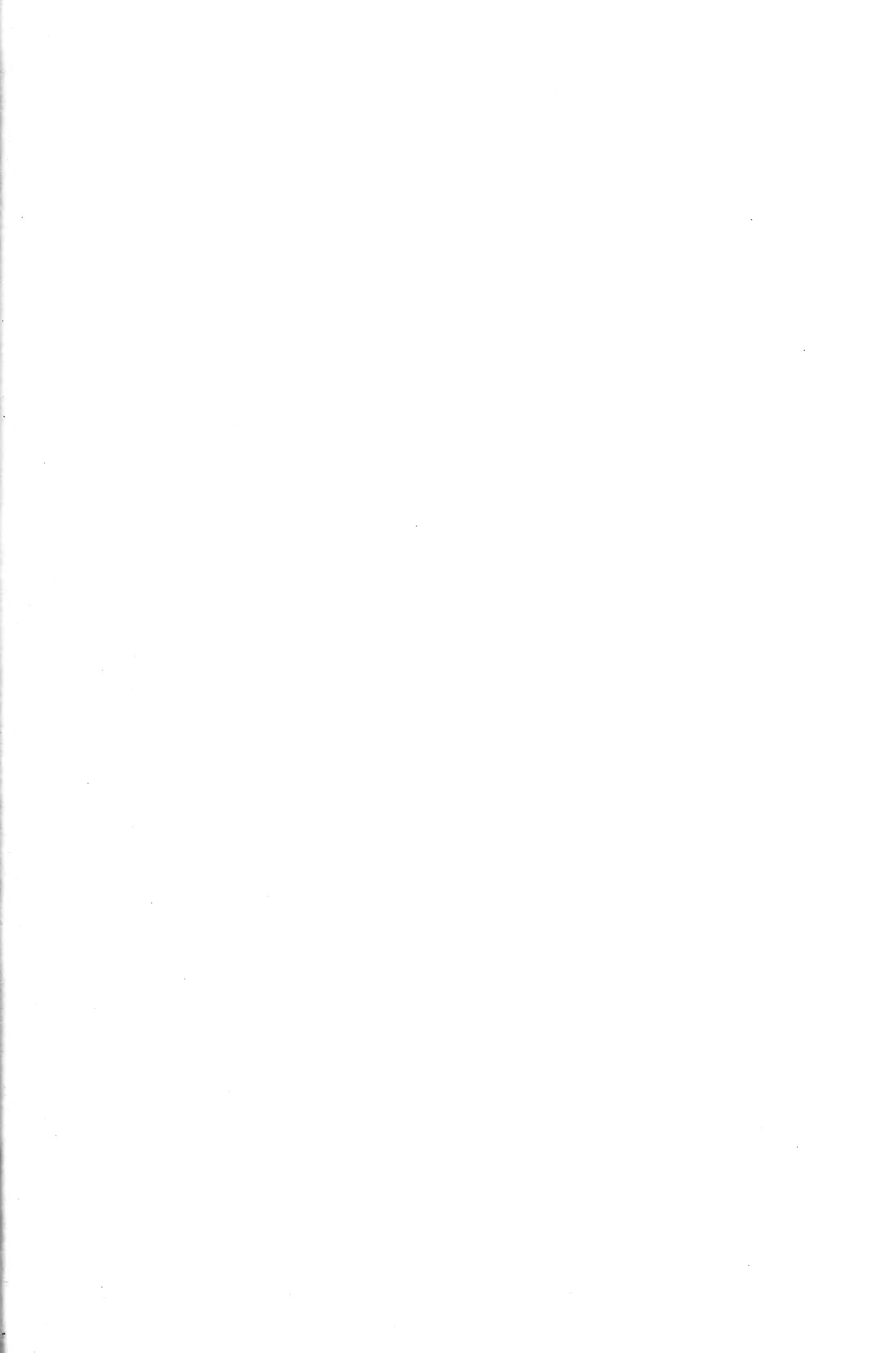
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